2011

AN ANALYSIS OF BEHAVIORAL FLEXIBILITY AND CUE PREFERENCE IN PIGEONS UNDER VARIABLE REVERSAL LEARNING CONDITIONS

Rebecca Marie Rayburn-Reeves
University of Kentucky, beckyreeves02@gmail.com

Recommended Citation

Rayburn-Reeves, Rebecca Marie, "AN ANALYSIS OF BEHAVIORAL FLEXIBILITY AND CUE PREFERENCE IN PIGEONS UNDER VARIABLE REVERSAL LEARNING CONDITIONS" (2011). *Theses and Dissertations--Psychology*. 1.
https://uknowledge.uky.edu/psychology_etds/1

STUDENT AGREEMENT:

I represent that my thesis or dissertation and abstract are my original work. Proper attribution has been given to all outside sources. I understand that I am solely responsible for obtaining any needed copyright permissions. I have obtained and attached hereto needed written permission statements(s) from the owner(s) of each third-party copyrighted matter to be included in my work, allowing electronic distribution (if such use is not permitted by the fair use doctrine).

I hereby grant to The University of Kentucky and its agents the non-exclusive license to archive and make accessible my work in whole or in part in all forms of media, now or hereafter known. I agree that the document mentioned above may be made available immediately for worldwide access unless a preapproved embargo applies.

I retain all other ownership rights to the copyright of my work. I also retain the right to use in future works (such as articles or books) all or part of my work. I understand that I am free to register the copyright to my work.

REVIEW, APPROVAL AND ACCEPTANCE

The document mentioned above has been reviewed and accepted by the student's advisor, on behalf of the advisory committee, and by the Director of Graduate Studies (DGS), on behalf of the program; we verify that this is the final, approved version of the student's dissertation including all changes required by the advisory committee. The undersigned agree to abide by the statements above.

Rebecca Marie Rayburn-Reeves, Student

Dr. Thomas R. Zentall, Major Professor

Dr. David Berry, Director of Graduate Studies

المنارة للاستشارات

www.manaraa.com

AN ANALYSIS OF BEHAVIORAL FLEXIBILITY AND CUE PREFERENCE IN PIGEONS UNDER VARIABLE REVERSAL LEARNING CONDITIONS

DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Science at the University of Kentucky

By
Rebecca Marie Rayburn-Reeves

Lexington, Kentucky

Director: Dr. Thomas R. Zentall, Professor of Psychology

Lexington, Kentucky

2011

ABSTRACT OF DISSERTATION

AN ANALYSIS OF BEHAVIORAL FLEXIBILITY AND CUE PREFERENCE IN PIGEONS UNDER VARIABLE REVERSAL LEARNING CONDITIONS

Behavioral flexibility, the ability to change behavior in accordance with the changing environment, was studied in pigeons using a series of reversal learning paradigms. All experiments involved a series of 5-trial sequences and I was interested in whether pigeons are sensitive to the reversal by switching to the other alternative after a single error. In Experiments 1 and 2, the overall probability of the two stimuli was equated over sequences, but the probability correct of the two stimuli changed across trials. In both experiments, subjects showed no sensitivity to the differences in sequence type. Instead they used the overall average of the probability of reinforcement on each trial as the basis of choice.

In the final two experiments, the likelihood that a reversal would occur on a given trial was equated such that there was an equal overall probability that the two stimuli would be correct on a given trial, but the overall probability of each stimulus being correct across sequences favored the second correct stimulus (S2). In Experiment 3, the overall probability of S2 correct was 80%, and results showed that subjects consistently chose S2 regardless of sequence type or trial number. In Experiment 4, the overall likelihood of S2 correct was 65%, and results showed that subjects began all sequences at chance, and as the sequence progressed, began choosing S2 more often.

In all experiments, subjects showed remarkably similar behavior regardless of where (or whether) the reversal occurred in a given sequence. Therefore, subjects appeared to be insensitive to the consequences of responses within a sequence (local information) and instead, seemed to be averaging over the sequences based on the overall probability of reinforcement for S1 or S2 being correct on each trial (aggregate information), thus not maximizing overall reinforcement. Together, the results of this series of experiments suggest that pigeons have a basic disposition for using the overall probability instead of using local feedback cues provided by the outcome of individual trials. The fact that pigeons do not use the more optimal information afforded by recent reinforcement contingencies to maximize reinforcement has implications for their use of flexible response strategies under reversal learning conditions.

KEYWORDS: Behavioral flexibility, Reversal learning, Discrimination learning, Probability learning, Timing

Rebecca Marie Rayburn-Reeves
Name

November 17, 2011
Date

AN ANALYSIS OF BEHAVIORAL FLEXIBILITY AND CUE PREFERNCE IN PIGEONS UNDER VARIABLE REVERSAL LEARNING CONDITIONS

BY

Rebecca Marie Rayburn-Reeves

Thomas R. Zentall
Director of Dissertation

David Berry, Ph. D.
Director of Graduate Studies

November 10, 2011
Date

DEDICATION

This paper is dedicated to my mother, Linda Rayburn, who taught me to never give up on myself, or the things I have a passion for, and to treat each challenge as an opportunity for greatness.

ACKNOWLEDGMENTS

I would like to thank Dr. Tom Zentall for his thoughtful guidance and ongoing patience, support, and expertise during the course of my graduate studies and especially through the dissertation process. I have learned from Dr. Zentall more in these past four years, both about the importance of comparative cognition to our understanding of evolution and of the rudiments of human behavior, and also about my own strengths as a researcher and as an academic. Thank you Z, for everything you have helped me to be.

I would also like to thank Dr. Philipp Kraemer for his advice and support during this last year of my graduate studies. He has been a wonderful person to work for and has been integral in developing and broadening my research skills in various aspects of psychology. It has been a pleasure to work with him.

I would like to extend a thank you to my other committee members, Dr. Ramesh Bhatt, Dr. Phil Crowley and Dr. Yang, as their advice and thoughtful comments about my work undoubtedly helped to create a more cohesive dissertation.

And of course, I would like to sincerely thank my cohorts, Dr. Holly Miller, Kristina Pattison, Jenifer Laude and Jessica Stagner, for their continued support and advice through the years, as well as their love and respect for me through it all.

I'd like to thank my family and friends as well, for without them, this experience would have been significantly more difficult. To my friend Judy Strosnider, for her amazing support and confidence in me. To my father, James Reeves, for being such an inspiration through my life and an amazing mentor. To my brother, Danny Rayburn-Reeves, for always challenging me to think critically and thoroughly about everything, and last but not least, to my mother, Linda Rayburn, for being my biggest supporter in life.

Finally, I would like to thank my partner, Brandi Lowe, for encouraging me through the final year of school and throughout the dissertation process. The challenges in life are welcomed when you have people in your life who make it all worthwhile and who support and love you even when the chips are down.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Section 1

Behavioral flexibility, described by Bond, Kamil, and Balda (2007), is the ability to respond rapidly to environmental changes and to be ready to seek out alternative solutions to problems encountered, if initial strategies are not effective. The term flexibility has been defined in various ways and has been used as a synonym for other concepts such as ‘adaptability’ or ‘plasticity’ (Peters, 1981). Stenhouse (1974) made use of the term flexibility when he described intelligence as “…the built-in flexibility that allows individual organisms to adjust their behavior to relatively rapidly changing environments” (p. 61). For comparative psychologists, the study of the ways in which animals learn about the environment and adjust their behavior in accordance with changing conditions is one way in which we can study the various aspects of their cognitive capabilities. Learning itself involves behavior that can be modified in order to adjust to new events in the environment based on previous experience. Papini and Ishida (1998) argued that studies investigating the comparative analysis of learning “…help us understand how learning capacities evolved, what function they serve, and what types of specialized abilities are there in different animals” (p. 3).

Discrimination Learning

The development of simple learning processes, such as discrimination learning, require the use of flexible behavior because the organism must learn to respond differentially to two stimuli on the basis of learning which stimulus results in reinforcement (Hulse, Egeth, & Deese, 1980). One type of discrimination learning problem is called a simultaneous discrimination, in which an organism is presented with two stimuli at the same time and is allowed to choose between them. In this task, choice of one stimulus (S+) is designated as correct and results in reinforcement, whereas choice of the other stimulus (S-) is incorrect and results in the absence of reinforcement. A subject is typically given repeated trials with the same contingencies in effect until it is responding to only the S+ stimulus. The learning of a discrimination can be explained by the build-up of associative strength (excitation) through the repeated pairing of a particular response (e.g., pecking a red key light) with reinforcement and the pairing of another response (e.g., pecking a green key light) with the absence of reinforcement (inhibition), through a process called trial and error learning. The number of trials it takes to reach a criterion of performance (e.g., 90% correct over a block of trials) can be used as a measure of the difficulty of the discrimination as well as the rate at which an individual is able to form an association between the stimulus and the response associated with the presence of that stimulus, which signals the availability of reinforcement.

The rate of simple discrimination learning may depend largely on certain aspects of the stimuli, (the modality, dimension, and how far apart the stimuli are along the chosen dimension), how the stimuli are presented (simultaneously or successively), response topography (key pecking or lever pressing), the methodological conditions (the inter-trial interval, delay of reinforcement) and reinforcement (duration and magnitude). Therefore, the rate of discrimination learning is susceptible to differences in various aspects of the procedure, which means that rates of learning across species tells us more about the appropriate elements of the procedure than the cognitive capacities of various species.

Discrimination Learning Set

A more complex discrimination learning procedure is one that presents a series of simple simultaneous discriminations over time. For example, in learning set procedures, an animal is presented with a simultaneous discrimination for a particular number of trials (e.g., 6), after which, a novel pair of stimuli are presented and a new discrimination must be learned. The benefit of providing multiple discrimination problems is to evaluate whether an animal can learn to use relevant information from previous discriminations to improve learning of new discriminations. For example, the learning set procedure, originally developed by Harlow (1949), tested monkeys on a series of simple simultaneous discrimination problems. Subjects were presented with a series of problems involving a choice between two three-dimensional objects. Choice of one object but not the other resulted in reinforcement. After a number of trials with the same discrimination, the objects were replaced with novel objects and, again, one of them was arbitrarily assigned as correct. In this manner, Harlow's monkeys received 344 pairs of novel objects. He observed that with early problems, subjects showed a gradual increase in choice of the correct stimulus over consecutive trials, a type of behavioral pattern indicative of trial and error learning. With later problems, however, Harlow (1949) observed that the monkeys consistently chose the correct stimulus on the second trial of a problem. He explained this change in accuracy as the acquisition of a 'learning set', which he defined as "learning how to learn efficiently in a situation an animal frequently encounters" (p. 51). Schrier and Thompson (1984) described 'learning set' formation as a steady, progressive improvement across problems, often to the point where only one trial is necessary to form the discrimination. That is, an animal that shows evidence of ‘learning set’ uses the information from Trial 1 as a basis for choice of stimulus on Trial 2 (Thomas, 2006). In this way, the animal learns that the information afforded by the outcome is the cue that allows the animal to maximize reinforcement on subsequent trials. This ability to maximize reinforcement after the first trial within a problem and across problems in a similar manner has been called as a “win-stay, lose-shift hypothesis” (Levine, 1965). Specifically, a win-stay, lose-shift strategy would be one in which the animal forms two specific rules; choose the stimulus to which responding was reinforced on the previous trial (win-stay), and switch to the alternative stimulus following a single unreinforced response (lose-shift). In this way, an animal must learn to treat each new problem independent of the last, even (and especially) when objects are used repeatedly over problems, because the value of that stimulus is based solely on the outcome of the first trial of a new problem. However, the animal must also learn that trials within a given problem are not independent of one another, as the outcome of the previous trial serves as a signal for the positive (S+) stimulus on the next. Harlow’s research demonstrates how complex forms of learning, such as win-stay/lose-shift rules, can gradually develop over time, when an animal is given multiple examples of a particular problem (Schrier, 1984).

Reversal Learning

A task related to learning set is reversal learning. Behavioral flexibility studied in reversal learning tasks measures sensitivity to changing reinforcement conditions involving a simple set of stimuli, typically two. The most frequently used reversal learning task is one in which two stimuli are simultaneously presented to a subject, with one stimulus arbitrarily assigned as correct and the other as incorrect. Subjects are presented with this pair of stimuli until they reach a criterion (e.g., 9 out of 10 consecutive trials correct) at which point the contingencies are reversed such that choice of the previously incorrect stimulus is now reinforced and choice of the previously correct stimulus is no longer reinforced. This new contingency remains in effect until subjects reach criterion, at which time the contingencies are again reversed. In this serial reversal task (also called habit reversal learning; see Bitterman, 1965) the same two stimuli are always presented but their values change with each reversal (Mackintosh, McGonigle, Holgate, & Vanderver, 1968). The question is, will animals show improved reversal learning with successive reversals. If one uses original learning as a baseline against which to measure improvement, one should be able to control for the difficulty of the original discrimination. That is, the degree of improvement relative to baseline should be a measure of the animal's cognitive flexibility (Bitterman, 1965, 1975). As with learning set tasks, the development of a win-stay/lose-shift rule would provide the maximum amount of reinforcement.

Serial reversals allow the same pair of stimuli to be used repeatedly, with just the change in contingency used as a basis of information for subsequent behavior. Therefore, an animal that can reverse rapidly (within a few trials) to the newly reinforced stimulus shows strong evidence that it has freed itself from the constraints of association-based trial and error learning and has learned instead to respond based on the immediate feedback associated with the most recent trial's outcome. That is, as with learning set tasks, the information afforded by the outcome serves as the cue for which response will be reinforced on the next trial. One advantage of learning set tasks is that there should be less interference from stimuli that appeared in previous problems; however, a disadvantage is that the discriminability across problems is likely to vary. Therefore, in learning set tasks, performance across problems is confounded with the level of discriminability of the stimuli within a problem. In the serial reversal task, however, the level of discriminability is held constant because the same two stimuli are used repeatedly across reversal problems. Serial reversal tasks also require a greater level of flexibility because subjects have to learn to inhibit responses to a stimulus that has been repeatedly paired with reinforcement and to respond to the other stimulus that has gone unreinforced for a number of trials. In serial reversal tasks, animals must therefore learn to ignore all other cues accept for the outcome following the stimulus to which the most recent response was made, which means that regardless of how many trials a particular response has gone reinforced, the first trial on which it is paired with nonreinforcement is a cue to switch to the alternative stimulus.

Research has shown that a variety of animals, including apes and monkeys (Beran et al., 2008; Warren, 1966), sea lions (Schusterman, 1966), horses (Martin, Zentall, & Lawrence, 2006), echidnas (Saunders, Chen, & Pridmore, 1971) rats (Bushnell & Stanton, 1991; Mackintosh & Holgate, 1969; Reid & Morris, 1992; Williams, 1972), weasels (Doty & Combs, 1969) crocodiles (Williams, 1967), turtles (Holmes & Bitterman, 1966), octopuses (Mackintosh & Mackintosh, 1964), and birds (Benowitz & Teng, 1973; Bond, Kamil, & Balda, 2007; Gossette, Gossette, & Riddell, 1966; Ploog & Williams, 2010; Wilson, 1978), show improvement across reversals, with some species showing greater improvement than others (Bitterman, 1969; Gonzalez, Brehend, & Bitterman, 1967; Woodward, Schoel, & Bitterman, 1971) and a few eventually often needing only one trial to learn the reversal of a discrimination (Dufort, Guttman, & Kimble, 1954; Staddon & Frank, 1974; Warren, 1965); however, the level of improvement varies both within and between species and depends also on the sensory modality of the stimuli, the nature of the stimuli within a modality, and the apparatus (Bullock & Bitterman, 1962; Deterline, 1957; Durlach & Mackintosh, 1986; Mackintosh, 1988; Mackintosh & Little, 1969; Mackintosh, Wilson, & Boakes, 1985). For example, it has been shown that rats show substantially more improvement in reversal learning tasks with olfactory stimuli than with visual stimuli (Duncan & Slotnick, 1990; Nigrosh, Slotnick, & Nevin, 1975; Slotnick, Kufera, & Silberberg, 1991; Slotnick & Katz, 1974).

Serial reversal tasks have taken many forms and have been used under a variety of different methodologies (Rajalakshmi & Jeeves, 1965). Studies requiring predetermined criterion levels of performance prior to a reversal have received the most attention (Bitterman, Wodinsky, & Candland, 1958; Cronholm, Warren, & Hara, 1960; Dews, 1957; Dufort, Guttman, & Kimble, 1954; Kay & Sime, 1962; Macphail, 1972; McDowell, Brown, & White, 1961; Pubols, 1956; Reid, 1958; Siedman, 1949; Wodinsky & Bitterman, 1957). Other serial reversal designs introduce reversals after a predetermined number of trials, regardless of the animal’s performance (Datta, Milstein, & Bitterman, 1960; Kirk & Bitterman, 1963; Mackintosh, et al., 1968; North, 1950; Pubols, 1956; Reid, 1958). Serial reversal tasks can also be studied using a between- or within-session design. A between-session design is one in which, upon reaching criterion (or a specified minimum number of trials), the session is either continued under the same contingencies of reinforcement until completed, or terminated until the following session, at which point the contingencies are reversed on Trial 1 of the following session. A within-session design is one in which the reversal occurs on the trial immediately following the one in which the subject reaches criterion (or a specified number of trials) on the previous discrimination. Both between- and within-session reversal learning have been studied and the general finding is that between-session reversal learning is typically an easier task to learn.

For example, Mackintosh et al. (1968) compared reversal learning performance in rats using either a between- or within-session reversal task in which the number of trials to the reversal was fixed. Two groups of rats were trained on a spatial discrimination in which reversals occurred on the first trial (between-session reversal) or in the middle of a 48-trial session (within-session reversal), such that, for the within-session group, each session began with the S+ stimulus that was reinforced for the last half of the previous session. It was found that both groups began sessions responding to both stimuli with a probability of .5; however, the between-session group performed better overall than the within-session group. The most popular explanation for the chance performance on Trial 1 for both groups is that subjects come to have an equal amount of experience with each stimulus being both an S+ and an S- on Trial 1 over sessions and, thus, an increase in proactive interference (interference from previous learning on new learning) develops (Gonzalez, Brehend, & Bitterman, 1967; Staddon & Frank, 1974). However, the most likely reason why the between-session group performed more accurately overall was because it was easier for the rats to make the same response throughout the session than to have to learn two different discriminations within the same session. In a sense, even though the only difference between the two procedures was the placement of the reversal (at the beginning or in the middle of the session), the fact that one required learning a single discrimination whereas the other required learning two opposite discriminations suggests that the within-session task was inherently more difficult. Other research using between versus within-session reversal learning has found similar results (Watson, Sullivan, Frank, & Stanton, 2005). In light of the differences in task difficulty, a comparison across groups in terms of performance seems inappropriate.

Another type of within-session reversal task is a midsession reversal task in which the same stimulus is correct for the first half of each session and the alternative stimulus is correct at the end of each session, which is a small, but important difference from previous within-session reversal tasks in which the S+ stimulus at the start of each session alternates between the two stimuli. If all sessions begin with the same S+ stimulus, subjects can learn over sessions to respond to that stimulus with a high level of accuracy, instead of beginning at chance and having to learn over trials which stimulus is initially correct that session. Therefore, performance should be relatively stable across the first half of the session up to the reversal point, whereas when beginning at chance, subjects might not reach a stable level of accuracy prior to the reversal.

Rayburn-Reeves, Molet & Zentall (2011) conducted a midsession reversal learning experiment using a simple simultaneous discrimination. In this task, two stimuli (red and green hues) were presented simultaneously on each trial, one being the correct (positive, S+) stimulus, and the other being the incorrect (negative, S-) stimulus. During the first half of each 80-trial session (Trials 1-40), responses to one stimulus, S1, were reinforced and responses to S2 were not (S1+, S2-). During the last half of the session (Trials 41-80), the contingencies were reversed such that responses to S2 and not S1 were reinforced for the remainder of the session (S1-, S2+). After 50 sessions of training, we found that subjects began to respond to S2 prior to the change in contingency (an anticipatory error) and also maintained responding to S1 after the change in contingency (a perseverative error). The results from sessions 41-50 (after stability had been reached) are plotted in Figure 1 as the percentage choice of the first correct stimulus as a function of trial number. The results for each of the ten pigeons' last ten sessions averaged across sessions can be seen in Figure 2. As can be seen in Figure 2, all ten subjects showed markedly similar behavior across the session, indicating that the function obtained in Figure 1 was not due to an averaging artifact. Almost all subjects showed a decline in accuracy between Trials 30-40 and very similar rates of switching to S2 (indicated by overlapping functions). This finding was interpreted as evidence that subjects were using the time into the session as a discriminative cue. Interestingly, subjects did not appear to be using the more immediately valid information afforded by the outcome of the previous trial(s) as a primary cue. Therefore, they did not obtain the maximal amount of reinforcement that they could have during the session. Although overall errors were quite low (less than 10%) on average, the fact that these errors persisted across sessions suggests that temporal control may be a difficult strategy to abandon. Had the pigeons used the information afforded by the outcome of their choice on the previous trial as a cue (a win-stay/lose-shift strategy), they could have obtained reinforcement on every trial except for the first trial in which the reversal occurred during the session, achieving much greater overall accuracy (less than 2% errors). Therefore, it seems that, when pitting feedback from reinforcement and its absence, along with time into the session, pigeons seem to rely more on time, suggesting that time may be a more natural cue than the recent history of reinforcement contingencies.

The anticipatory errors made by the pigeons suggest that subjects were using a reference memory for the reversal event occurring during the session, and using a time-

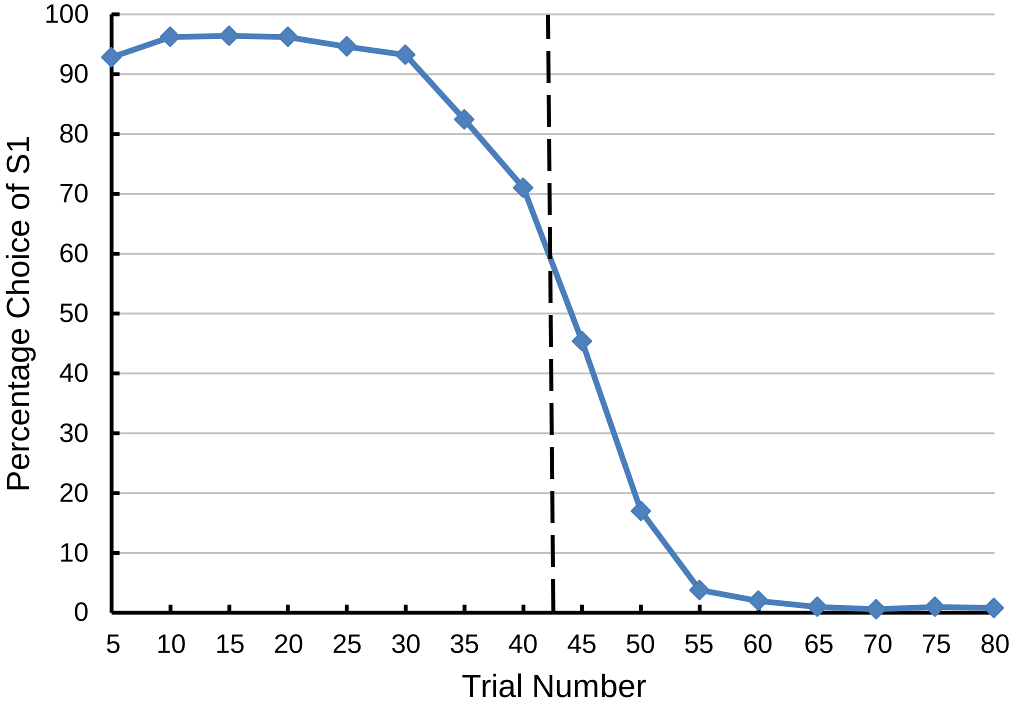

Figure 1. Percentage choice of S1 as a function of trial number averaged across subjects and sessions 41-50. Data are plotted in blocks of 5 trials. The black dotted line indicates the reversal location.

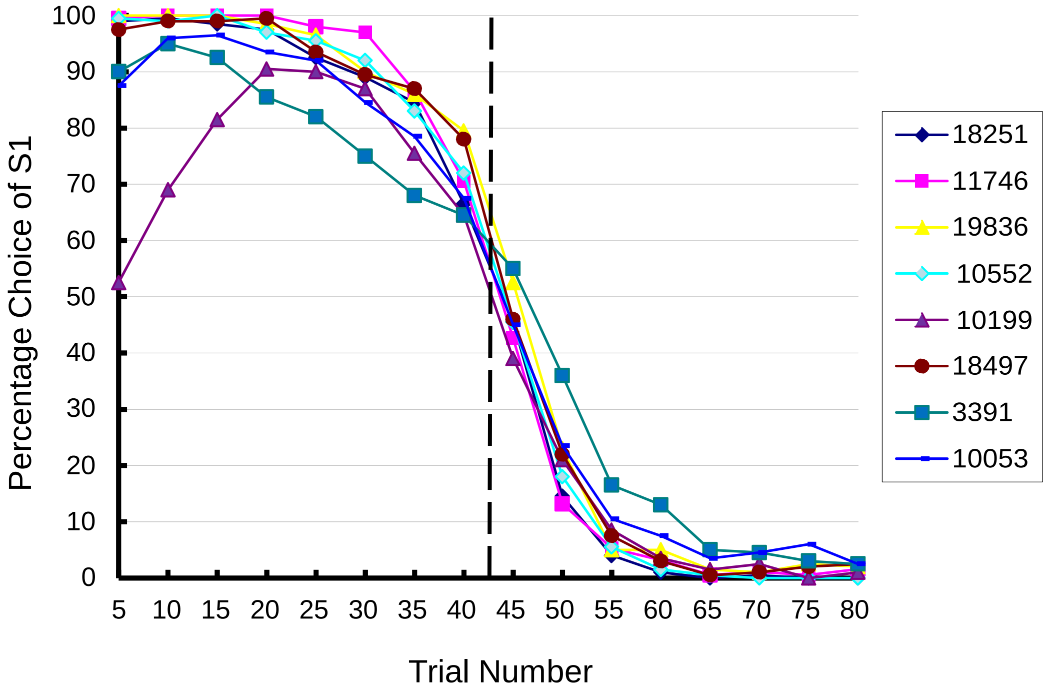

Figure 2. Percentage choice of S1 as a function of trial number for individual subjects averaged across sessions 41-50. Data are plotted in blocks of 5 trials. The black dotted line indicates the reversal location.

based strategy to gauge the point at which the reversal would occur within the session. Interestingly, if pigeons were anticipating the reversal event, it would seem that, once the event occurred, they would rapidly switch to the other stimulus; however, the number of perseverative errors was strikingly similar to the number of anticipatory errors. A possible reason for the continued responses to S1 after the reversal could be that pigeons were being reinforced on a partial reinforcement schedule prior to the reversal, thereby making the reversal less salient or discriminable than if they had continued to choose S1 prior to the reversal (continuous reinforcement).

As the pigeons appeared to use the time into the session as a cue rather than basing their response on the consequences of their choice on the most recent trials, a second preliminary experiment (Rayburn-Reeves, Molet, & Zentall, 2011; unpublished data) was conducted to reduce the validity of time as a cue to reverse and therefore, to encourage the pigeons to be more sensitive to the consequences of their choice on the immediately preceding trials. Thus, if timing was adopted as a strategy in the previous experiment because it could easily be used, then discouraging timing as a strategy might encourage a strategy that affords more sensitivity to the reinforcement contingencies. In the second preliminary experiment, the point at which the reversal occurred within the session was varied across sessions in an unpredictable manner. The reversal could occur in one of five different temporal locations during the session (after Trial 10, 25, 40, 55, or 70) with one location randomly selected on each session. In this task, adopting a win-stay/lose-shift strategy would still result in an overall accuracy score of 98.75% (79/80 correct each session). The same subjects were used and given a considerable amount of training (100 sessions; 20 at each reversal location). Results showed that when the reversal occurred early in the session (after Trial 10) subjects made few anticipatory errors but they continued to make many perseverative errors. That is, they continued to respond to S1 long after the reversal had occurred (see Figure 3). Additionally, when the reversal occurred late in the session (after Trial 70) subjects made a substantial number of anticipatory errors to the point where, just prior to the change in contingency (when S1 was still correct), subjects were responding to S2 approximately 65% of the time. The large amount of overlap seen across reversal locations suggests that subjects were still using the time within the session as a cue for stimulus choice on a given trial; however, the fact that the reversal locations produced separate functions means that there was some sensitivity to the reinforcement contingencies. As compared with the overall percentage correct for a win-stay/lose-shift strategy (98.75), the average percentage correct for all birds on this task was 81.93.

In a third experiment (Rayburn-Reeves, et al., 2011; Experiment 2), a new group of pigeons (N = 8) were tested on the variable reversal procedure for 100 sessions, as in the second experiment. In the third experiment we found that, when trained from the start on the variable reversal procedure, pigeons showed greater sensitivity to the reinforcement contingencies than when tested on the variable reversal procedure after being trained on the consistent procedure (an average percentage correct of 86.67 as opposed to 81.93); however, a large number of perseverative and anticipatory errors still were found when the reversal came early in the session and a large number of anticipatory errors occurred when the reversal came late in the session (see Figure 4).

Previous research has shown that increasing the response requirement associated with a particular stimulus can help to increase the saliency of the reinforcement

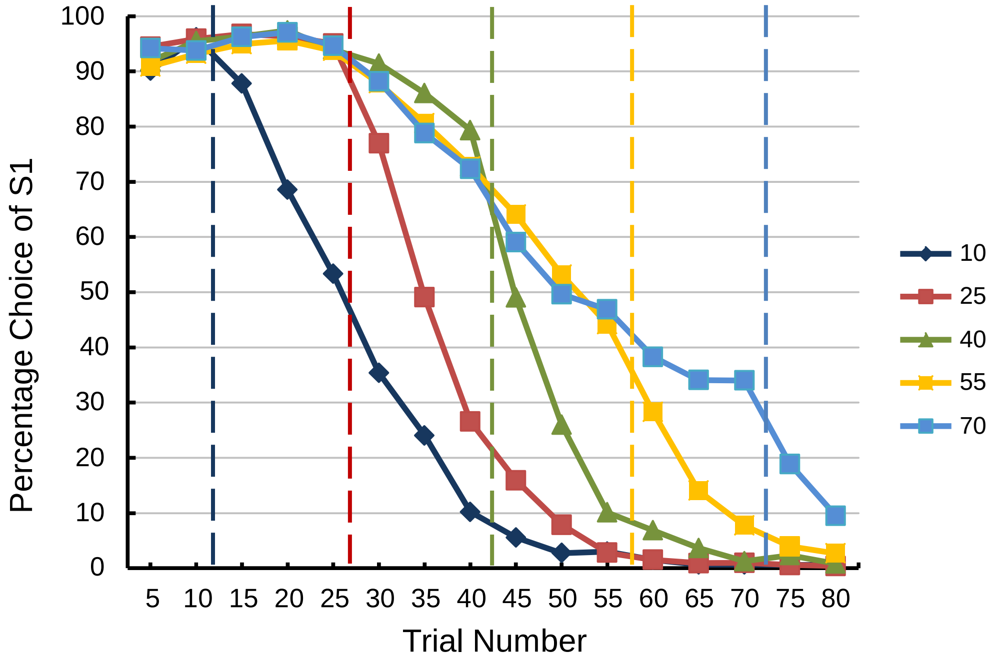

Figure 3. Percentage choice of S1 as a function of trial number averaged across subjects and Sessions 75-100 (last 5 sessions at each reversal location). Each dotted line represents the reversal location corresponding to the data line matching in color.

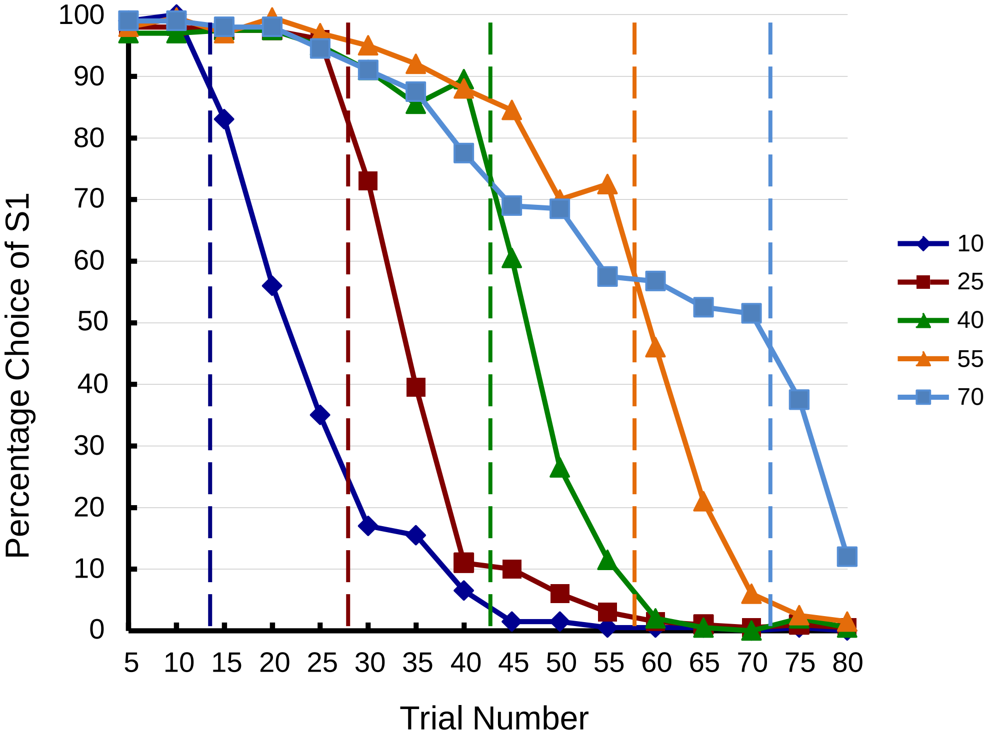

Figure 4. Percentage choice of S1 as a function of trial number averaged across subjects and Sessions 75-100 (last 5 sessions at each reversal location). Each dotted line represents the reversal location corresponding to the data line matching in color.

contingencies associated with that stimulus (Rayburn-Reeves, Miller, & Zentall, 2010) and there is evidence that it may facilitate serial reversal learning in pigeons (Williams, 1971). Therefore, we conducted an additional midsession reversal experiment (Rayburn-Reeves, Molet, & Zentall, 2010; Experiment 3) in which the response requirement was increased from 1 to 20 pecks (the first key to which 20 pecks were made determined the pigeon's choice). As in the second and third preliminary experiments, subjects were given 100 sessions with the reversal point varying across sessions. The results indicated, however, that the increase in response requirement did not significantly affect the accuracy of the birds (overall average percentage correct was 83.81). That is, subjects showed very similar results as those found in the third preliminary experiment with the variable reversal procedure, when only one peck was required to either stimulus (see Figure 5). The percentage errors as a function of reversal location for the variable reversal procedure are shown in Figure 6. As can be seen in the figure, the birds that received prior training with the reversal occurring in the middle of the session (red line) showed the most number of errors across all reversal locations, indicating that the prior experience interfered with their performance. For the other two experiments in which subjects were naïve to the task, the FR1 group (blue line) performed more accurately than the FR20 group (green line) across all reversal locations. Therefore, the increase in response requirement did not facilitate performance on the task and, in fact, seemed to make the task more difficult.

In our final preliminary experiment, we tested the hypothesis that it may be more difficult for the pigeons to remember the color of the most recently chosen stimulus (as

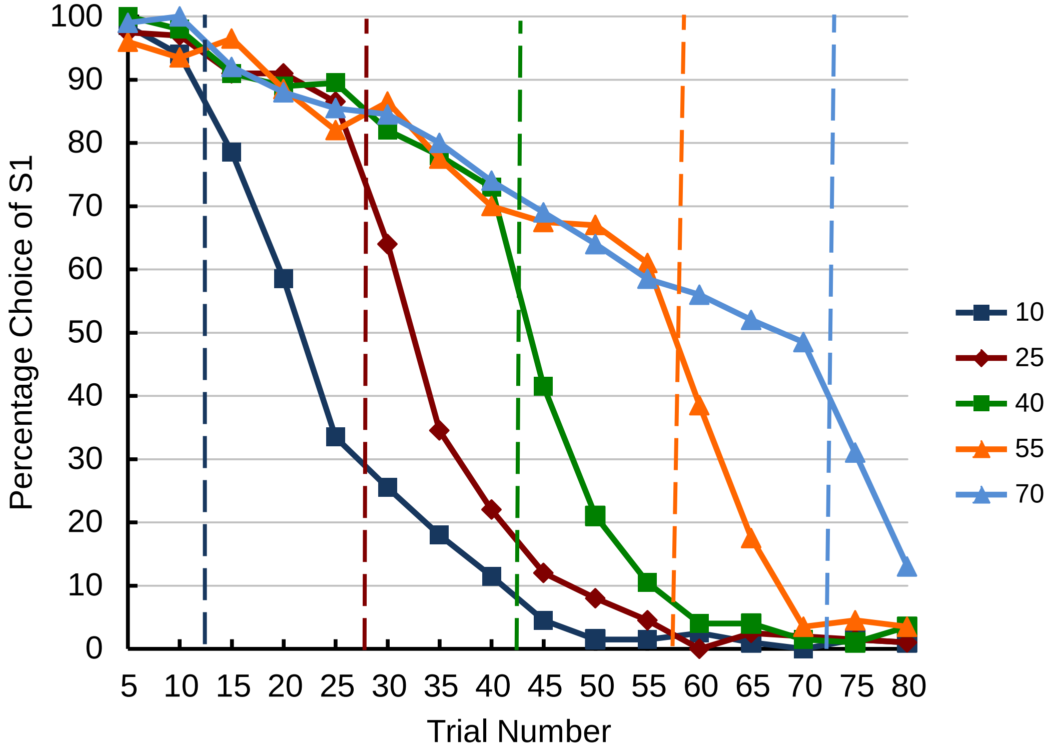

Figure 5. Percentage choice of S1 as a function of trial number averaged across subjects and Sessions 75-100 (last 5 sessions at each reversal location). Each dotted line represents the reversal location corresponding to the data line matching in color.

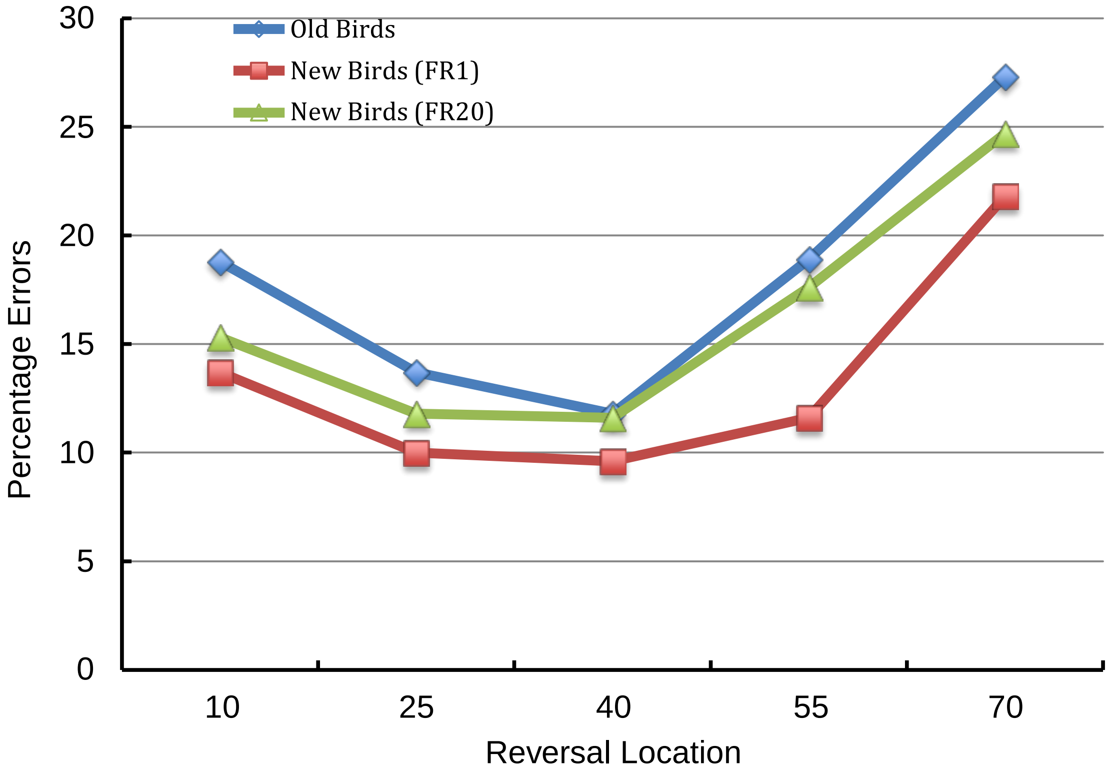

Figure 6. Percentage errors as a function of reversal location averaged across subjects for preliminary Experiments 2, 3, and 4.

well as the outcome on the preceding trials) by changing the task to a spatial discrimination (Rayburn-Reeves, Stagner, Kirk, & Zentall, in press; Experiment 1). In this experiment, a white key light was displayed on the left and right side keys. One side key was designated as S1 and the other as S2 and the reversal occurred after Trial 40. Pigeons were given 50 training sessions. Results showed that the pigeons' performance on the spatial reversal task was quite similar to their performance on the visual reversal task (overall percentage correct was 91.35). That is, they still made many anticipatory errors prior to the reversal as well as many perseverative errors after the reversal (see Figure 7). For comparison purposes, the data from the initial experiment using a visual discrimination task has been included in the figure. Therefore, whether tested on a visual or a spatial discrimination, pigeons continued to use the time into the session as a cue rather than base their response solely on the feedback from the preceding response and therefore they used a cue that was sub-optimal compared with cue that potentially would have provided them with considerably more reinforcement.

Given the results from the initial experiments in our lab using the simultaneous within-session reversal procedures, it appears that pigeons are not able to refrain from using average time (or number of trials) into the session as a cue for reversal of the discrimination. In the limit, the efficient use of the local history of reinforcement, if applied to this single-reversal simultaneous discrimination, would result in the use of a win-stay/lose-shift response strategy. That is, if subjects based their choice on each trial on the outcome of the choice from the preceding trial, it would have resulted in a high level of accuracy (ideally only one error per session).

The following experiments were proposed to investigate what cues pigeons use

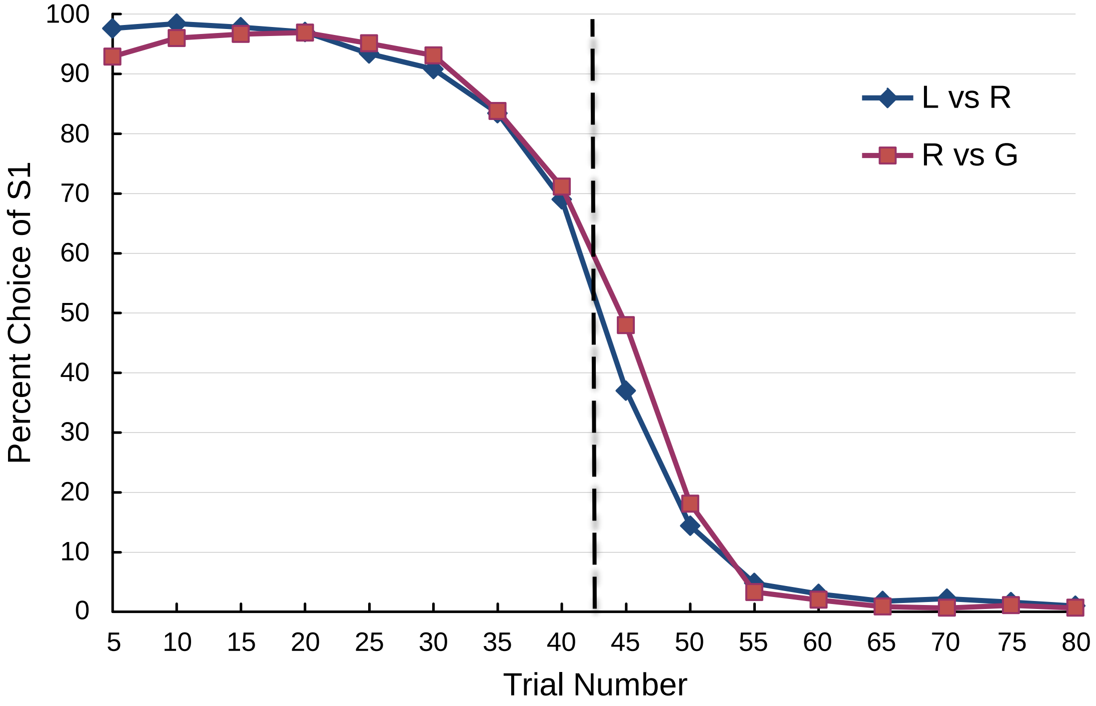

Figure 7. Percentage choice of S1 as a function of trial number averaged across subjects and Sessions 41-50 for both the spatial (blue line) and visual (red line) midsession reversal tasks. Data are plotted in blocks of 5 trials. The black dotted line indicates the reversal location.

when performing tasks of this kind and to determine if pigeons can be encouraged to use the outcome of the most recent trials as a basis for their future behavior in that session. These experiments attempted to maximize the saliency of each trial's outcome to encourage the pigeons to be more sensitive to the consequences of their behavior on the most recent trials.

In our initial experiments with pigeons, each session was comprised of 80 trials. The fact that there were so many trials might have reduced the saliency of the consequences of a response on any given trial. This may have contributed to the subjects' use of timing to help predict the reversal instead of the contingencies of reinforcement associated with the stimuli on a given trial. After all, it worked reasonably well, resulting in reinforcement ranging from 81-90% across all the within-session reversal tasks. However, the use of timing resulted in less than optimal performance because subjects began reversing too early and maintaining responses to the previously reinforced stimulus even after multiple non-reinforced trials.

With 80 trials per session, each incorrect response results in only a small reduction in overall reinforcement. In the following experiments, each session consisted of a series of 5-trial sequences to emphasize the local history of reinforcement. With a 5-trial sequence, an incorrect response would result in a reduction of 20% of the possible reinforcements, which may increase the saliency of the reinforcement contingencies on each trial. Additionally, because the number of trials was reduced from 80 to 5, we were able to have a session in which multiple sequences were presented with long delays between sequences to make the sequences discriminable. In this manner, we were able to present several reversals per session as opposed to just a single reversal each day. With the 5-trial sequences, it was possible to increase the number of reversal events from 1 to 16 while still keeping the number of trials per day at 80. It was our hypothesis that the increase in exposure to reversal events would possibly allow the subject to learn to attend to the change in contingencies as a cue to reverse.

Section 2

Experiment 1

Variable reversal procedure without end points

The first proposed experiment used a variable reversal procedure similar to that used in the second preliminary experiment, but with only five trials in each sequence. Using only five trials in the initial experiment allowed us to see more directly whether the reduction in trials within a session would create more sensitivity to local reinforcement history when the reversal was somewhat unpredictable. In Experiment 1, the reversal point could occur at one of four different locations during each sequence (after Trial 1, 2, 3 or 4). Therefore, in this paradigm, just as in the variable reversal paradigm with 80 trials, S1 was always correct at the start of the session (Trial 1 for the 5-trial sequences and Trials 1-10 for the 80-trial sessions) and S2 was always correct at the end of the session (Trial 5 for the 5-trial sequences and Trials 71-80 for the 80-trial sessions). Additionally, the reduction in the number of trials from 80 to 5 allowed us to assess the previous hypothesis that pigeons were using the time from the start of the session and averaging across sessions to estimate the overall probability that S1 or S2 was correct on a given trial, as they appeared to be doing in the variable reversal procedures.

Method

Subjects

Four White Carneaux pigeons (*Columbia Livia*) and two Homing Pigeons (*Columbia Livia*) served as subjects. The White Carneauxs ranged between 2 to 12 yrs old, while the Homing pigeons were approximately 1 yr old at the start of the experiment. All subjects had experience in previous unrelated studies involving simultaneous color discriminations but had not been exposed to a reversal learning task. Throughout the experiment, the pigeons were maintained at 85% of their free-feeding weight. They were individually housed in wire cages with free access to water and grit in a colony room that was maintained on a 12-hr/12-hr light/dark cycle. The pigeons were maintained in accordance with a protocol approved by the Institutional Animal Care and Use Committee at the University of Kentucky.

Apparatus

The experiment was conducted in a BRS/LVE (Laurel, MD) sound attenuating standard operant test chamber measuring 34 cm high, 30 cm from the response panel to the back wall, and 35 cm across the response panel. Three circular response keys (3 cm in diameter) were aligned horizontally on the response panel and were separated from each other by 6.0 cm but only the side response keys were used in these experiments. The bottom edge of the response keys was 24 cm from the wire-mesh floor. A 12-stimulus in-line projector (Industrial Electronics Engineering, Van Nuys, CA) with 28-V, 0.1-A lamps (GE 1820), that projected red and green hues (Kodak Wratten Filter Nos. 26 and 60, respectively), was mounted behind both side response keys. Mixed-grain reinforcement (Purina Pro Grains - a mixture of corn, wheat, peas, kafir and vetch) was provided from a raised and illuminated grain feeder located behind a horizontally centered 5.1 x 5.7 cm aperture, which was located vertically midway between the response keys and the floor of the chamber. Reinforcement consisted of 2 s access to mixed grain. A white house light, which provided general illumination between sequences, was located in a central position on the ceiling of the chamber. The experiment was controlled by a microcomputer and interface located in an adjacent room.

Procedure

At the start of each sequence, one side key was illuminated red and the other green; the same as in previous experiments using red and green hues. The location of the hues (left vs. right) varied randomly from trial to trial. The red and green hues were randomly assigned as S1 and S2 stimuli over subjects such that for half of the subjects, red was designated as S1 and green as S2 and for the other half, green was S1 and red was S2. On a given sequence, the reversal point randomly occurred on one of four different trials in each 5-trial sequence (after Trial 1, 2, 3, or 4), thereby making the overall probability of S1 and S2 correct equal across each session (see Table 1). A single response to the correct stimulus resulted in both stimuli turning off and 2 s access to grain followed by a 3 s dark inter-trial interval whereas a response to the incorrect stimulus turned off both stimuli and resulted in a 5 s dark inter-trial interval. Immediately following the inter-trial interval, each hue was randomly presented on either side key, indicating the start of the next trial. Each 5-trial sequence was separated by a 1-minute inter-sequence interval during which the house light was illuminated. Subjects were tested on the variable reversal paradigm for a total of 16 sequences per session (4 at each sequence type) for a total of 60 days (240 sequences at each reversal point for a total of 960 reversals).

Results

The results of Experiment 1 indicate that when pigeons are given a session with multiple sequences in which the point of the reversal is made variable across sequences, but where S1 is always correct on Trial 1 and S2 is always correct on Trial 5, the percent choice of S1 is systematically reduced as a function of trial number, regardless of the trial on which the reversal occurs (see Figure 8). Whether the reversal occurred after Trial 1, 2, 3, or 4, the shape of the choice functions for each reversal location was almost identical. Figure 8 shows the percentage choice of S1 as a function of trial number in the sequence averaged across subjects for Sessions 41-60 combined (a total of 80 reversals for each reversal point; 240 reversals total per subject). A repeated measures analysis of

Table 1

Experiment 1: Probability of S1 Correct as a Function of Sequence Type and Trial Number

Sequence Type	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	S1 Corr. Per Sequence
1	S1	S1	S1	S1	S2	80%
2	S1	S1	S1	S2	S2	60%
3	S1	S1	S2	S2	S2	40%
4	S1	S2	S2	S2	S2	20%
S1 Corr. Per Trial	100%	75%	50%	25%	0%	

Note. S1 = the first correct stimulus. S2 = the second correct stimulus.

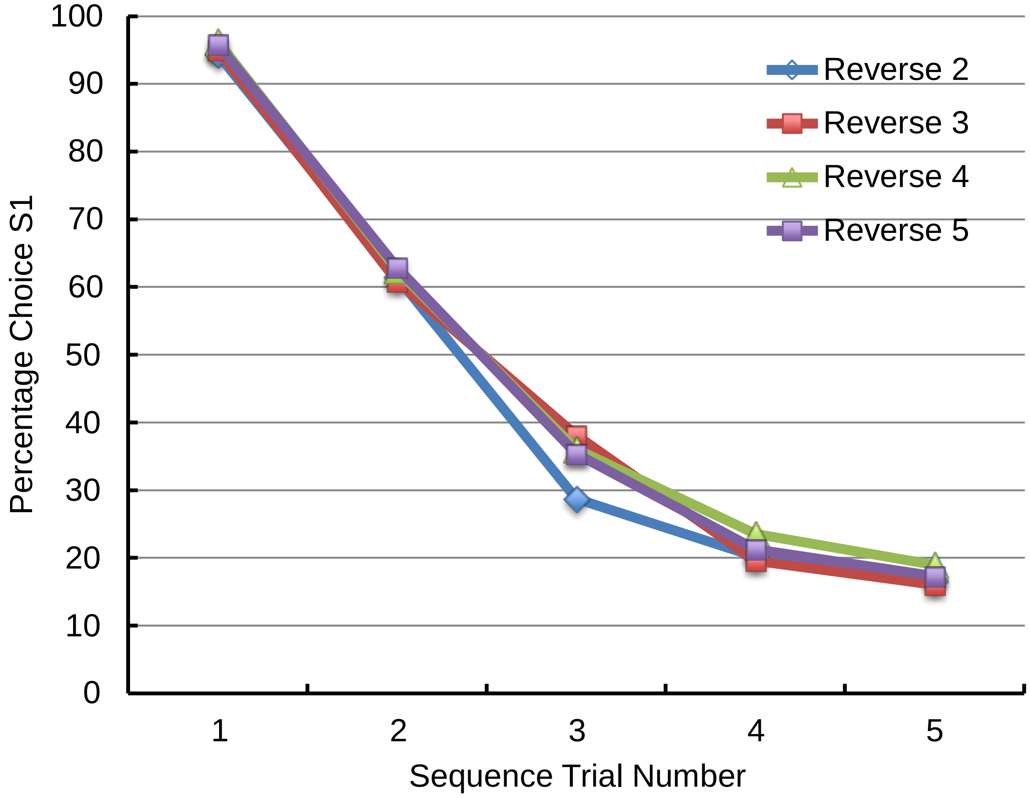

Figure 8. Experiment 1. Percentage choice of S1 as a function of sequence trial number averaged across subjects and across Sessions 41-60 for each sequence type.

variance (ANOVA) was conducted on the four reversal locations as a function of the five trials within a sequence, and we found a significant main effect of trial number *F*(4, 20) = 51.218, *p* < .0001, but no main effect of reversal location *F*(3, 15) = 2.04, *p* = .151, and no trial x reversal interaction *F*(12, 60) = .681, *p* = .763.

Due to the lack of variability, we collapsed across reversal locations to take a measure of the average percentage choice of S1 on each trial as compared with a theoretical measure of the overall probability of S1 being correct as a function of trial number (see dashed line in Figure 9). This corresponds to the probability of being correct for each trial location in the sequence pooled over each of the 16 sequences per session. That is, without regard for the feedback from reinforcement or its absence from preceding trials in the sequence. A single sample t-test was conducted on the data from each trial relative to the mean overall probability that S1 was correct, independent of the location of the reversal in the sequence. The average choice of S1 (M, 95.36; SEM, .459) was significantly lower than the mean for Trial 1 (100%), *t*(5) = -10.09, *p* < .001; however, the average choice of S1 was not significantly different on Trial 2 (M, 61.93; SEM, 7.28) than the overall mean (75%), *t*(5) = -1.80, *p* = .13. On Trial 3, the average choice of S1 (M, 34.58; SEM, 5.26) was again significantly lower than the overall mean (50%), *t*(5) = -2.93, *p* = .03; however on Trial 4, the average choice of S1 (M, 21.15; SEM, 4.23) was not significantly different from the overall mean (25%), *t*(5) = -0.91, *p* = .403. Finally, on Trial 5, the average choice of S1 (M, 17.24; SEM, 4.42) was significantly higher than the overall mean (0%), *t*(5) = 3.90, *p* = .01.

Data for individual subjects are depicted in Figure 10. Each figure is plotted as the percentage choice of S1 as a function of sequence trial number for sessions 41-60. The data were pooled over Sessions 41-60 due to the lack of variability or improvement as a function of experience with the task and to gain power. Overall, there was some between-

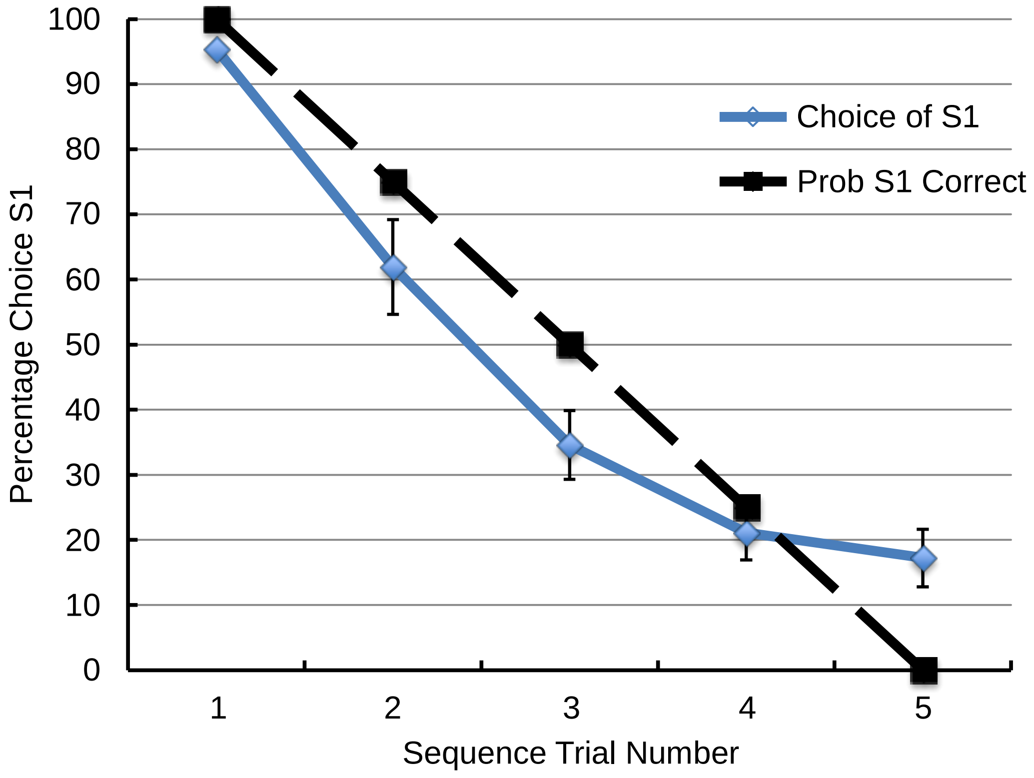

Figure 9. Experiment 1. Percentage choice of the first correct stimulus as a function of trial number collapsed across sequence types. The black dotted line indicates the overall probability of S1 correct as a function of trial number independent of reversal location.

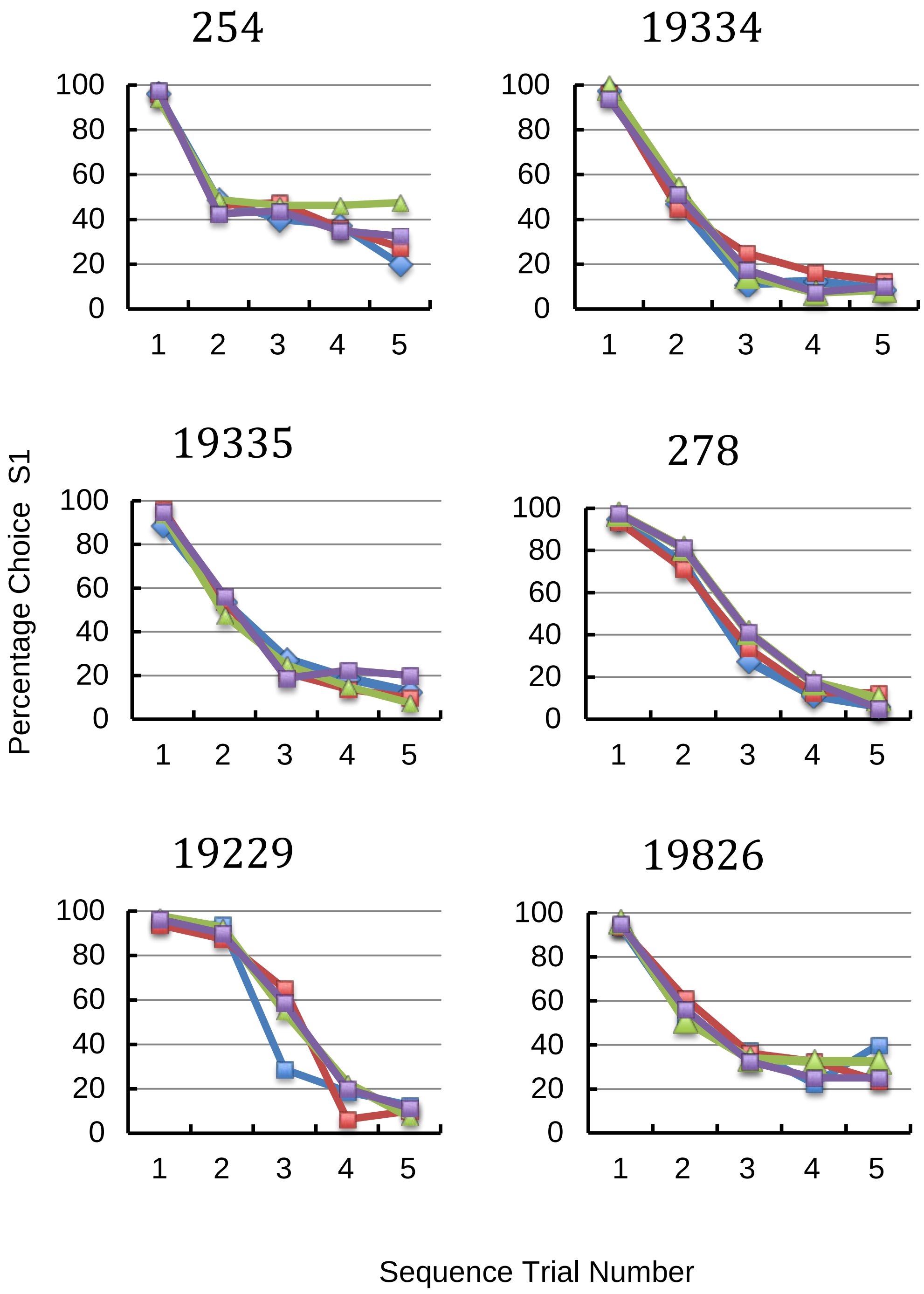

Figure 10. Experiment 1. Percentage choice of S1 as a function of sequence trial number for individual subjects averaged across Sessions 41-60 for each sequence type.

subject variability for when subjects began to shift responses to S2 during a sequence; however, there was hardly any within-subject variability across reversal locations. Additionally, overall percentage correct for the two homing pigeons (M= 69.125) was not significantly different from that of the white carneauxs (M= 70.407), *t* < 1. Only one of the six subjects showed some sensitivity to the within-sequence reinforcement contingencies. Specifically, as one can see in Figure 10, the functions depicted for each reversal location for subject 19229 varied on different trials, somewhat consistent with the reversal location for the sequence. For example, for the sequences in which the reversal occurred after Trial 1, the percentage choice of S1 dropped from 94% on Trial 2 (the first feedback trial) to 29% on Trial 3, while the functions for the other reversal locations dropped to only 60%. Similarly, for the sequences in which a reversal occurred after Trial 2, the percentage choice of S1 dropped from 65% on Trial 3 to 6.2% on Trial 4, whereas for functions for reversals after Trials 3 or 4, the percentage choice of S1 averaged 21% on Trial 4.

Discussion

It was hypothesized that with a 5-trial sequence in which the reversal point could occur at one of four locations within the sequence (after Trial 1, 2, 3, or 4), but in which S1 was always correct on Trial 1 and S2 was always correct on Trial 5, subjects may show greater sensitivity to the local feedback cues due to the fact that the reversal may be more salient with fewer trials. Because responses to S1 were always reinforced for the first trial of every sequence, subjects learned to consistently respond to that stimulus at the start of every sequence. Regardless of when the reversal occurred during a given sequence, results showed that on average, percentage choice of S1 on Trial 1 was 95.4%. Therefore, the 1-minute inter-trial interval was sufficient to allow proper discrimination across sequences. After the first trial, because the reversal point could not be consistently predicted across sequences, subjects should have continued to respond to S1 until the first nonreinforced trial. However, because a reversal always occurred during each sequence, subjects began to anticipate this event and therefore were more likely to respond to S2 as the sequence progressed.

The fact that all pigeons showed similar functions with increasing trials in the sequence suggests that they were not sensitive to the reversal location in a given sequence. Therefore, it appears that pigeons (with the exception of 19229) did not use the information afforded by the most recent trial's outcome as a basis choice of stimulus, but instead appeared to use a reference memory for the overall probability that S1 or S2 would be correct on a given trial within the sequence. On Trial 2, four out of the six subjects began to choose S2 at almost the same rate as S1, whereas only two subjects showed a preference for S1 on Trial 2 (the actual probability that S1 was correct on Trial 2 was .75). The main effect of trial number suggests that as the trial number increased in a sequence, the preference for responding to S2 also increased. The overall probability that S1 would be correct on Trials 1, 2, 3, 4, or 5 when averaged across reversal locations was 1.0, .75, .50, .25 and 0. Therefore, if subjects were solely responding to the overall probability that S1 was correct on a given trial, the functions should not have been significantly different from the overall probability at each trial. However, it was found that choice of S1 on Trials 1, 3, and 5 were significantly different from the overall probability, suggesting that the subjects were using an additional cue aside from the overall probability of reinforcement given the trial number. On Trial 1, the main reason there was a significant difference between the percentage choice of S1 (95.4%) and the overall probability of S1 correct (100%) was because there was very little between-subject variability. The significant difference between the percentage choice of S1 on

Trial 3 (34.58%) and the overall probability of S1 correct (50%) is a bit more difficult to explain, but may have been due to uncertainty as to which trial the subject was on, Trial 3 or Trial 4. It is also possible that a bias to choose S2 may be analogous to foraging in patches in which one patch becomes less and less likely to provide food, whereas another patch becomes more and more likely. In this sense, S2 becomes more likely to be correct as the sequence progresses. It is possible that pigeons may be biased in this circumstance to begin to choose the stimulus that more often than not gets reinforced over time. Finally, the significant difference between the percentage choice of S1 (17.24%) and the overall probability of S1 correct on Trial 5 (0%) could also be due to the uncertainty about which trial the subject was on, Trial 5 or Trial 4.

If subjects had adopted the win-stay/lose-shift strategy to solve this task, and had learned to begin sequences responding to S1 on Trial 1, they would have received all but one reinforcer during each sequence for an average of 80% correct overall (refer to Table 1). An average of the percentage correct overall across subjects and reversal locations was 69.97% (Range = 63.13-75.5%), significantly worse than the 80% that could have been obtained with a win-stay/lose-shift rule $t(5) = -4.9$, $p < .005$. Additionally, the functions for each of the reversal locations would have looked different from one another (they would not have overlapped). All but one of the subjects, however, showed similar percentage choice responses to S1 as a function of trial number for all reversal points. Only 19229 showed an effect of nonreinforcement on the preceding trial (see Figure 10). For sequences with the reversal occurring on Trial 2, 19229 showed a significant increase in responses to S2 on Trial 3 than on the other sequence types. However, late reversals (reversals occurring on Trial 4 or 5) were treated similarly, suggesting a lack of discriminability between reversals occurring on those two trials. This lack of discriminability was consistent across subjects and suggests that pigeons were having difficulty discriminating whether they were on Trial 4 or 5. This difficulty is consistent with previous research that has shown that pigeons have difficulty discriminating more than three sequential events in counting studies (Rayburn-Reeves, Miller, & Zentall, 2010). The apparent lack of discriminability between Trials 4 and 5 may be responsible for the greater than expected choice of S1 on Trial 5 (given the 0% probability of reinforcement for choice of S1 on Trial 5).

The results of Experiment 1 indicate that, when the reversal location across sequences varies in an unpredictable manner, and when S1 is always correct on Trial 1 and S2 on Trial 5, pigeons do not use the information afforded by the local contingencies of reinforcement as a basis for choice of responses to S1 or S2 on subsequent trials. Instead, it appears that pigeons use the average probability of reinforcement of S1 across a large number of sequences to gauge the likelihood that S1 is correct on a particular trial. It is interesting to note the significant bias to choose S2 on Trial 3 as opposed to the overall probability of S2 being correct on that trial. Overall, however, it appears that pigeons largely are basing their responses on the overall probability of reinforcement associated with the trial in the sequence and it is clear that the location of the reversal in the sequence is not being used as a basis for stimulus choice.

Section 3

Experiment 2

Variable Reversal with end points

In Experiment 1, because a reversal always occurred during a sequence, the probability of a reversal increased as the pigeon progressed through the sequence (if it had not occurred by Trial 4 it would certainly occur on Trial 5). The results of Experiment 1 suggest that pigeons began to anticipate the reversal by choosing S2 more often than S1 with increasing trials in a sequence. Thus, pigeons in Experiment 1 did not adopt a win-stay/lose-shift strategy, nor did they seem sensitive to the information provided by local reinforcement on a given sequence. The second proposed experiment included two additional sequence types in which a reversal did not occur. In Experiment 2, one sequence type was added in which a reversal never occurred (S1 remained correct throughout the entire sequence). A second sequence type was added in which S2 was correct for the entire sequence (see Table 2). The main reason for the addition of these two sequence types was so that reversals during the sequence were no longer inevitable. Therefore, because the reversal could not be predicted to occur on any given sequence (S1 might be correct for all five trials), it was thought that subjects might therefore show less of a bias to choose S2 as a sequence progressed. This manipulation intended to help to reduce the number of anticipatory errors in such a way that Experiment 1 could not, while also equating the overall probability of S1 and S2 correct. Interestingly, the adoption of a win-stay/lose-shift strategy, where subjects began sequences responding to S1 on Trial 1 (the most optimal WSLS strategy), would result in an overall percentage correct of 83.33.

Method

Subjects

Four White Carneaux pigeons (*Columbia Livia*) ranging in age from 2 to 12 yrs and two homing pigeons (*Columbia Livia*), which were approximately 1 yr old at the start of the experiment, served as subjects. All subjects had had previous experience similar to the pigeons in Experiment1. Subjects were housed and maintained in the same manner as in Experiment 1.

Apparatus

The experiment was conducted using the same apparatus as in Experiment 1.

Procedure

The procedure was the same as in Experiment 1 with the exception that the reversal point could occur after one of six points in the sequence (after Trial 0, 1, 2, 3, 4, or 5), instead of one of four points, using a semi-random order. Each reversal point was not repeated for more than two consecutive sessions. A reversal point after Trial 0 means that the reversal occurred before the sequence began and responses to S2 were reinforced for the entire sequence. A reversal point that occurred after Trial 5 indicates that responses to S1 were reinforced for the entire 5-trial sequence. Subjects were tested on the variable reversal paradigm for 18 sequences per day for a total of 60 days (180 sequences for each reversal location; a total of 1080 reversals overall).

Results

The results of Experiment 2 indicate that when pigeons trained with sequences in which the point of the reversal is made variable across sequences with no certainty of S1 or S2 being correct on any given trial, the percentage choice of S1 was systematically

Table 2

Experiment 2: Probability of S1 Correct as a Function of Sequence Type and Trial Number

Sequence Type	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	S1 Corr. Per Sequence
1	S1	S1	S1	S1	S1	100%
2	S1	S1	S1	S1	S2	80%
3	S1	S1	S1	S2	S2	60%
4	S1	S1	S2	S2	S2	40%
5	S1	S2	S2	S2	S2	20%
6	S2	S2	S2	S2	S2	0%
S1 Corr. Per Trial	83.33%	66.67%	50.00%	33.33%	16.67%	

reduced as a function of trial number, regardless of the trial on which the reversal occurred. Additionally, whether the reversal occurred after Trial 0, 1, 2, 3, 4, or 5 (no reversal), the shape of the functions for each reversal location was almost identical, similar to the results of Experiment 1. Figure 11 shows the percentage choice of S1 as a function of sequence trial number averaged across subjects and over Sessions 41-60 (a total of 60 reversals for each reversal point; 360 reversals total per subject). A repeated measures analysis of variance (ANOVA) was conducted on each of the six sequence types as a function of the five trials within a sequence, and we found a significant main effect of trial number, *F*(4, 20) = 28.76, *p* < .0001, but no significant main effect of reversal location, *F*(5, 25) = 2.095, *p* = .10, nor was there a significant trial x reversal interaction, *F*(20, 100) = 1.413, *p* = .134.

Again, due to the lack of variability across reversal locations, as was found in Experiment 1, the data were pooled over reversal locations to assess the average percentage choice of S1 on each trial as compared with a measure of the overall probability of S1 correct as a function of trial number (see dashed line in Figure 12). This corresponds to the probability of being correct for each trial location in the sequence pooled over each of the 18 sequences per session. That is, without regard for the feedback from reinforcement or its absence from preceding trials in the sequence. A single sample t-test was conducted for each trial relative to the hypothetical mean associated with the overall probability of S1 correct. The average choice of S1 (M, 85.22; SEM, 6.38) was not significantly different than the hypothetical mean for Trial 1 (83.33%), *t*(5) = .2963, *p*= .77; however, the average choice of S1 was significantly lower on Trial 2, (M, 44.09; SEM, 4.98) than the overall probability that S1

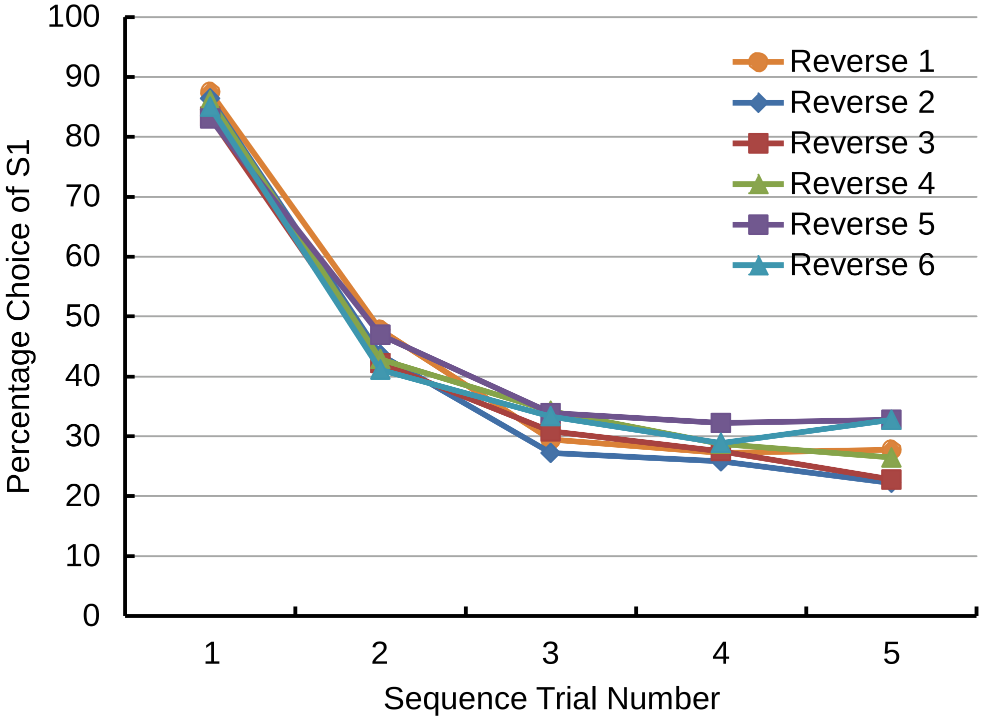

Figure 11. Experiment 2. Percentage choice of S1 as a function of sequence trial number averaged across subjects and across Sessions 41-60 for each sequence type.

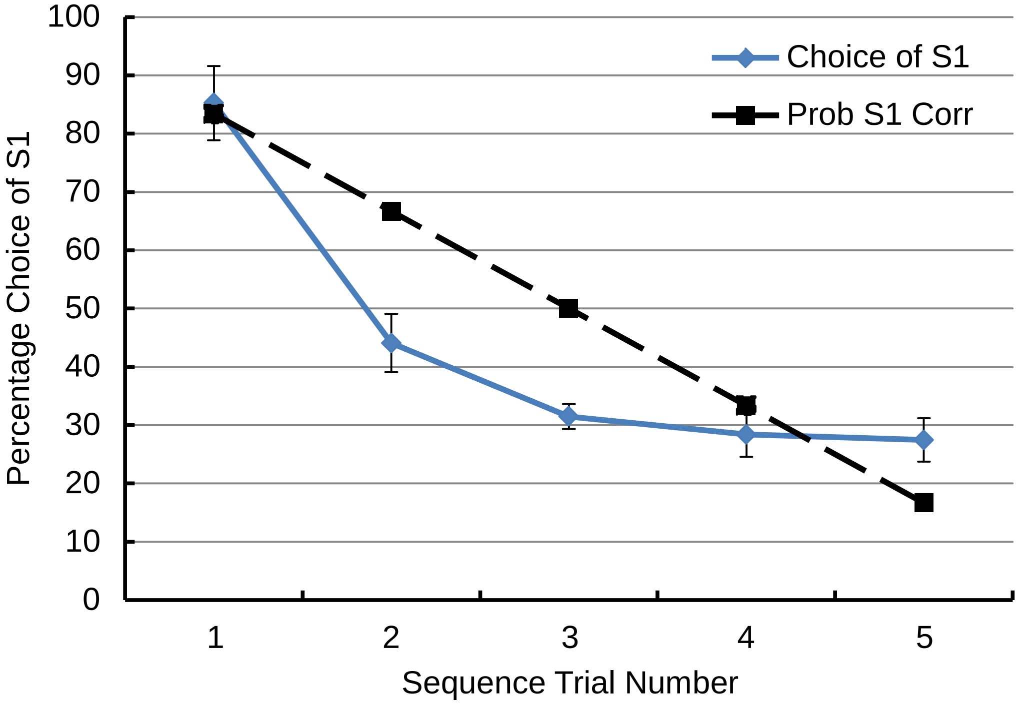

Figure 12. Experiment 2. Percentage choice of the first correct stimulus as a function of trial number collapsed across sequence types. The black dotted line indicates the overall probability of S1 correct as a function of trial number independent of reversal location.

was correct on Trial 2 (66.67%), *t*(5) = -4.53, *p* = .006. On Trial 3, the average choice of S1 (M, 31.49; SEM, 2.15) was again significantly lower than the overall probability that S1 was correct on Trial 3 (50%), *t*(5) = -8.61, *p* = .0003; however on Trial 4, the average choice of S1 (M, 28.40; SEM, 3.84) was not significantly different from the overall probability that S1 was correct on Trial 4 (33.33%), *t*(5) = -1.284, *p* = .256. Finally, on Trial 5, the average choice of S1 (M, 27.47; SEM, 3.73) was significantly higher than the overall probability that S1 was correct on Trial 5 (16.67%), *t*(5) = 2.89, *p* = .03.

Data for individual subjects are depicted in Figure 13. Each figure is plotted as the percentage choice of S1 as a function of sequence trial number for sessions 41-60. The data from Sessions 41-60 were pooled due to the lack of variability or improvement as a function of experience with the task at that point in training. Overall, as in Experiment 1, there was some between-subject variability for when subjects began to shift responses to S2 during a sequence; however, as can be seen in Figure 13, there was hardly any within- subject variability across reversal locations for any subject. Additionally, overall percentage correct for the two homing pigeons (M, 58.42) was not significantly different from that of the white carneauxs (M, 60.02), *t*(34) = .039, *p* = .70.

Five out of the six birds showed a large preference for S1, choosing it over 80 percent of the time on Trial 1, whereas only one subject (Bird 15926) showed indifference to choice of S1, choosing it 55 percent of the time on Trial 1 (see Figure 13); however, Bird 15926 was relatively indifferent between S1 and S2, regardless of the reversal location or trial number. Two of the subjects (Birds 18798 and 2361) showed similar functions beginning with a large preference for S1 on Trial 1 and responding increasingly more often to S2 as the sequence progressed. The other

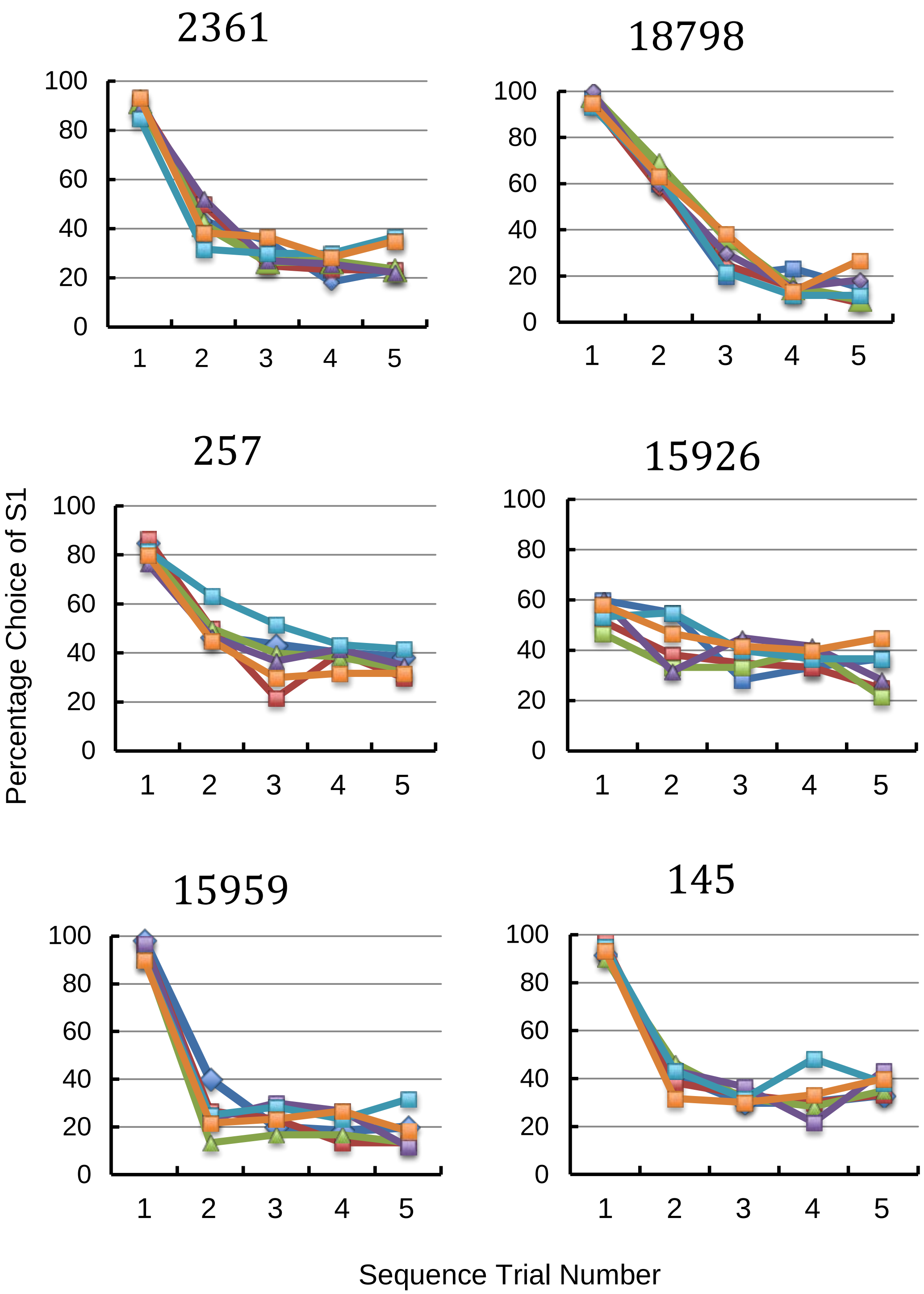

Figure 13. Experiment 2. Percentage choice of S1 as a function of sequence trial number for individual subjects averaged across Sessions 41-60 for each sequence type.

three subjects showed a large drop from Trial 1 to Trial 2 in choice of S1 and maintained a relatively stable preference for S2 throughout the remaining trials, showing a floor effect due to strong anticipation of S2.

In Experiment 2, if subjects had adopted the most appropriate win-stay/lose-shift strategy to solve this task (choosing S1 on Trial 1), they would have received an average of 83.33% correct overall; however, the overall average percentage correct was 59.49%, significantly worse than the maximum amount of reinforcement possible $t(5) = -16.68$, $p < .0001$. Therefore, the use of an overall probability of S1 or S2 correct on a given trial, with no sensitivity to differences in the reversal location across sequences, resulted in less than maximum reinforcement.

Discussion

Adding in sequences in which a reversal never occurred or in which it occurred before the sequence began did not decrease anticipatory responses, in spite of the fact that the reversal was no longer inevitable (that is, it was no longer predictable that S2 would be correct on Trial 5). There was no effect of early reversals (reversals occurring on Trial 1 or 2) on preference for S1 or S2 on later trials. If subjects responded to S1 on Trial 1 and were not reinforced, this information could have been used as a basis for reversing and for maintaining responses to S2 for the duration of the sequence, but it was not. That is, every sequence type produced similar functions for the percentage choice of S1 across trials for each subject. Therefore, as in Experiment 1, subjects were not treating the sequence types independently of one another. The average choice of S1 on Trial 1 was not significantly different from the overall probability that S1 would be correct across all sequence types, indicating that subjects may have been matching the overall probability of reinforcement on this trial. The average choice of S1 on Trials 2 and 3 showed significant anticipation to S2 relative to the overall probability of S2 being correct on those trials, indicating a significant anticipatory bias for S2. By Trial 4, the average choice of S2 did not significantly differ from the overall probability of S2 correct across sequence types. Finally, the average choice of S2 on Trial 5 was significantly higher than the overall probability of S2 correct, indicating a possible lack of sensitivity to the trial number subjects were on at the time. That is, as in Experiment 1, subjects may have been uncertain whether they were on the last trial (for which there was a mean percentage S1 correct of 16.7%) or the next to last trial (for which there was a mean percentage S1 correct of 33.3%), thereby choosing S1 on Trial 5 more than would be expected, given the overall probability of S1 being correct, and treating Trials 4 and 5 similarly.

The results of Experiment 2 indicate that, when the location of the reversal was both variable and uncertain (2 sequence types did not involve a reversal), pigeons did not adopt a strategy indicative of win-stay/lose shift, but instead appeared to average across sequences to estimate the overall likelihood that S1 or S2 would be correct on a given trial within the sequence. It is possible that the anticipatory bias was due to uncertainty about where the subjects are in the sequence, but the fact that there was a bias to anticipate as opposed to perseverate (choosing S1 more often than S2) is interesting, especially because there was equal probability of S1 and S2 being correct across all sequences. It is not obvious why there should be a bias to choose S2 significantly more often than S1 on any given trial, especially when the contingencies of reinforcement had not reversed. It is equally interesting to speculate about why pigeons show no sensitivity to early reversals considering the fact that once the reversal occurred, S2 was correct for the remainder of the sequence. The fact that in both Experiment 1 and 2, there were significantly more responses to S2 on Trial 3 than would be expected if subjects were matching the probability correct for that trial, may suggest that they may have been uncertain about what trial they were on in the sequence. As with the results of Experiment 1, the bias might also be attributed to the fact that, over time, S2 becomes more attractive due to its increasing value as an S+ stimulus, whereas S1 becomes less valued over time or trials. That is to say, the overall probability of S2 correct on Trials 1-5 was 16.67%, 33.33%, 50%, 66.67%, and 83.33%, respectively. This overall value of S2 (the overall probability of reinforcement) from Trial 1 to Trial 2 is doubled and then increased again by 50% from Trial 2 to Trial 3. As each trial progresses, the likelihood that S2 is correct is increased, but by a decreasing proportion to the overall probability from the last trial. Therefore, it may be that the proportion of the increase in value of S2 from Trial 1 to Trial 2, coupled with the decreasing value of S1 across trials, also contributed to the bias to choose S2 more often than what would have been predicted by the overall probability of S2 correct.

Section 4

Experiment 3

Variable reversal with equal probability of reversal on each trial

The first proposed experiment was aimed at directly comparing the differences in variable reversal learning when the number of trials in a given session was reduced from 80 to five. The second proposed experiment was aimed at reducing the anticipatory responses seen in all previous experiments with pigeons, when a reversal always occurred during a session, by eliminating the certainty that a reversal would always occur on the last trial if it had not already occurred. Although the first and second experiments were also aimed at reducing the use of timing as a source of information for subsequent behavior, it can be argued that time within the 5-trial sequence had not been completely eliminated as a cue. In both experiments, the probability that S2 would be correct increased systematically over the trials in a sequence, ending with a 100 percent chance on Trial 5 in Experiment 1 and an 83.3 percent in Experiment 2. This increasing probability might have been the reason that subjects were biased to choose S2 more often than S1 after Trial 1, given that no subject showed evidence of being sensitive to the local history of reinforcement.

Therefore, in Experiment 3, instead of each reversal point occurring an equal number of times throughout the experiment, the frequency of each reversal point was manipulated using a probability algorithm (hazard function) that controlled for the use of timing throughout the sequence such that the probability of a reversal or no reversal was equal at all trials. To accomplish this, the experiment consisted of 30 blocks of 32 sequences (2 sessions per block; 16 sequences per session). In each block of sequences there was one sequence with a reversal occurring after Trial 4 and one sequence with no reversal, 2 sequences with a reversal after Trial 3, 4 sequences with a reversal after Trial

2, 8 sequences with a reversal after Trial 1, and 16 sequences in which the reversal occurred before the sequence began, meaning S2 was correct for the entire sequence (see Table 3). This manipulation ensured that after each trial, there was an equal probability that the reversal would occur or would not occur on the next trial.

Method

Subjects

Four White Carneaux pigeons (*Columbia Livia*) ranging in age from 2 to 12 yrs and 2 homing pigeons (*Columbia Livia*), which were approximately 1 yr old at the start of testing, served as subjects. All subjects had similar experience in previous experiments but had no prior experience in reversal learning tasks. Subjects were housed and maintained in the same manner as in Experiments 1 and 2.

Apparatus

The experiment was conducted using the same apparatus as in the previous experiments.

Procedure

The procedure in Experiment 3 was the same as in Experiment 2 with the exception that the number of presentations of each sequence type per block varied according to a hazard function that controlled for the probability of a reversal occurring after each trial, as outlined above. There were 2 sessions per block, with 16 sequences per session. For the first block, there were 8 sequences with a reversal on Trial 1, 4 with a reversal on Trial 2, 2 with a reversal on Trial 3, 1 with a reversal on Trial 4, and 1 with a reversal on Trial 5. For Block 2, the same number of sequences were presented across the session for reversals on Trials 1, 2, 3, and 4, but there was no reversal on Trial 5, instead there was a no-reversal sequence (reversal after Trial 5). Subjects were tested for

Table 3

Experiment 3: Probability of S1 Correct as a Function of Sequence Type and Trial Number

Sequence Type	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	S1 Corr. Per Seq.	Seq. Per Block
1	S1	S1	S1	S1	S1	100%	1
2	S1	S1	S1	S1	S2	80%	1
3	S1	S1	S1	S2	S2	60%	2
4	S1	S1	S2	S2	S2	40%	4
5	S1	S2	S2	S2	S2	20%	8
6	S2	S2	S2	S2	S2	0%	16
S1 Corr. Per Trial Over Each Block	50%	25%	12.5%	6.67%	3.13%		32 Total

a total of 60 sessions (480 sequences with a reversal on Trial 1, 240 with a reversal on Trial 2, 120 with a reversal on Trial 3, 60 with a reversal on Trial 4, 30 with a reversal on Trial 5, and 30 with a no reversal sequence) for a total of 960 sequences.

Results

The results of Experiment 3 indicate that, when the reversal location was varied such that the probability of a reversal or no reversal was equal across trials, all subjects showed a significant bias to respond to S2. Only on Trial 1 did the percentage choice of S1 deviate significantly from 0 (see Figure 14). As in previous experiments, due to the lack of variability, we pooled the data over reversal locations to compare the average percentage choice of S1 on each trial with the overall probability of S1 being correct as a function of trial number (see Figure 15). A single sample t-test was conducted for the data from each trial relative to the overall probability that S1 was correct. The average choice of S1 (M, 16.08; SEM, 9.34) was significantly lower than the overall mean for Trial 1 (50%), $t(5) = -3.63$, $p = .02$; and the average choice of S1 (M, .938; SEM, .90) was also significantly lower than the overall mean for Trial 2 (25%), $t(5) = -26.85$, $p < .0001$. On Trial 3, the average choice of S1 (M, 1.11; SEM, .95) was again significantly lower than the overall mean (12.5%), $t(5) = -11.94$, $p < .0001$; and on Trial 4, the average choice of S1 (M, .938; SEM, .90) was also significantly lower than the overall mean (6.25%), $t(5) = -5.93$, $p = .002$. Finally, on Trial 5, the average choice of S1 (M, 1.22; SEM, .88) was not significantly different from the overall mean (3.13%), $t(5) = -2.18$. $p = .08$.

Data for individual subjects averaged across sessions 41-60 for each of the six sequence types appear in Figure 16. Four of the six subjects (birds 245, 278, 10534 and 19389) chose S2 almost exclusively throughout sessions 41-60. Only two subjects (birds

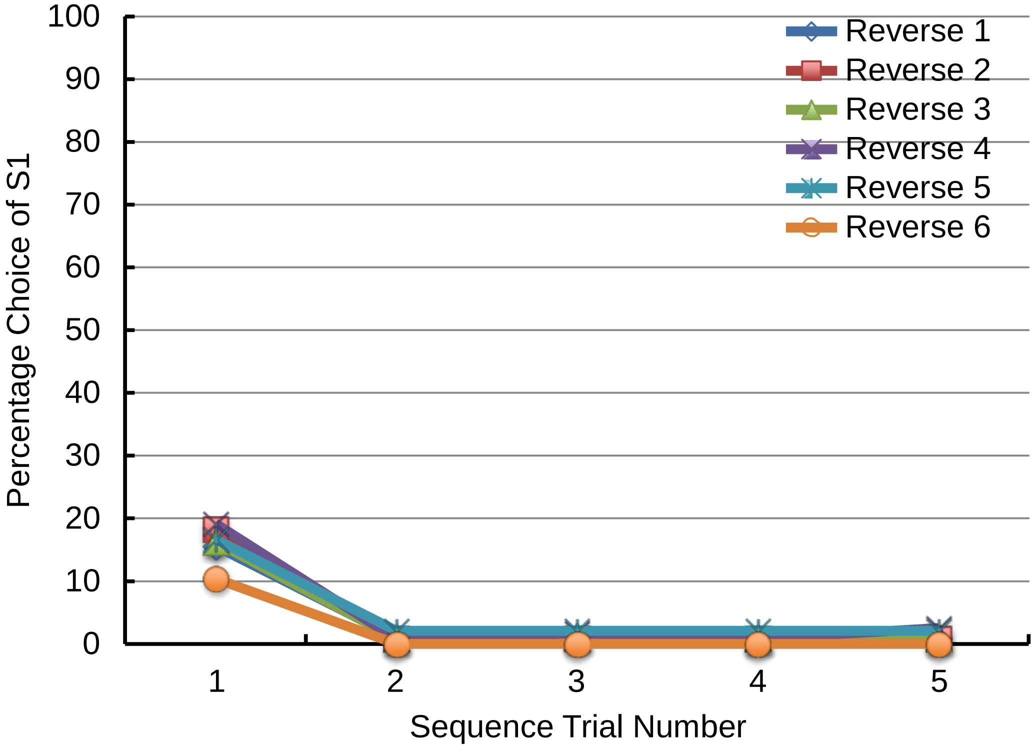

Figure 14. Experiment 3. Percentage choice of S1 as a function of sequence trial number averaged across subjects and across Sessions 41-60 for each sequence type.

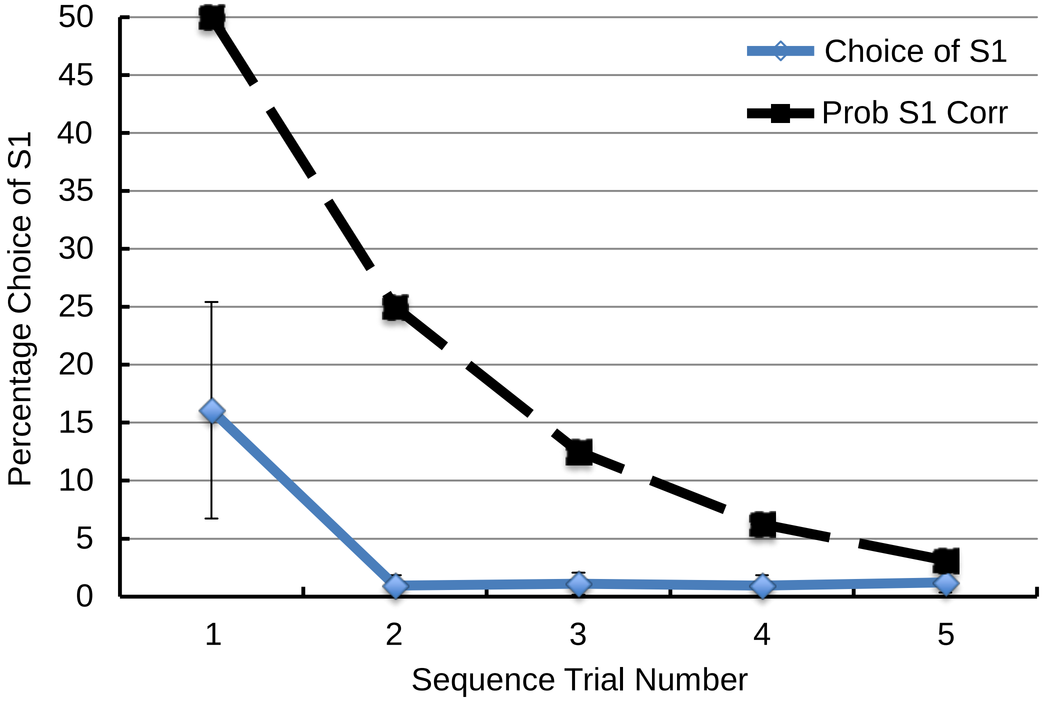

Figure 15. Experiment 3. Percentage choice of the first correct stimulus as a function of trial number collapsed across sequence types. The black dotted line indicates the overall probability of S1 correct as a function of trial number independent of reversal location.

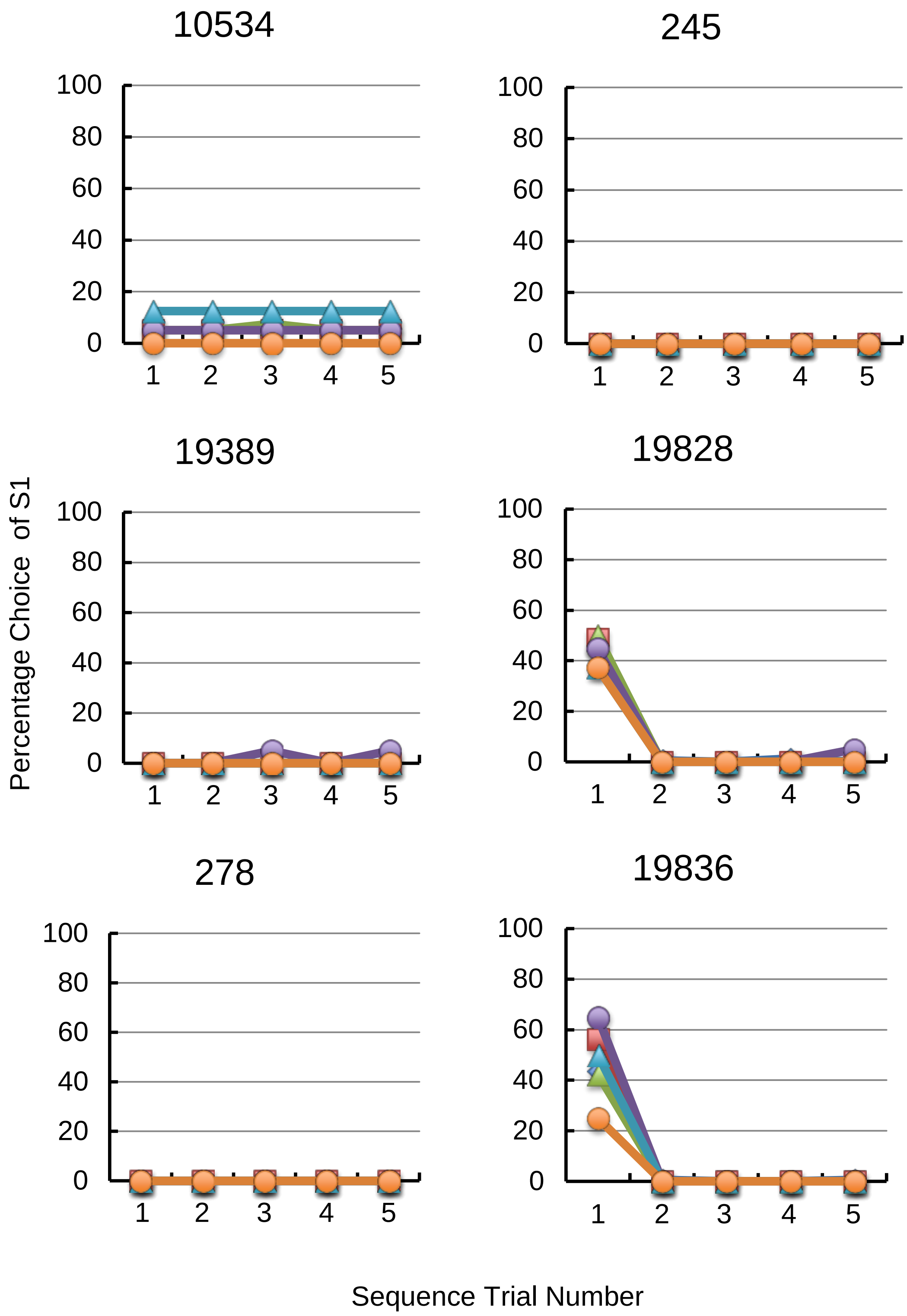

Figure 16. Experiment 3. Percentage choice of S1 as a function of sequence trial number for individual subjects averaged across Sessions 41-60 for each sequence type.

19828 and 19836) showed any responding to S1 and this was only on the first trial, on which responses to S1 and S2 were approximately equal, and equal to the overall probability that S1 was correct.

Discussion

Although the manipulation of frequency of the point of reversal conducted in Experiment 3 allowed for the removal of timing as a valid cue by using a hazard function to produce an equal probability of a reversal occurring at each trial in the sequence, the total number of trials in which a response to S1 and S2 were reinforced varied dramatically such that a response to S2 was reinforced 80.6% of the time. Therefore, subjects did not learn to reverse their choice and instead developed a systematic preference for S2.

These results suggest that, when the benefits of timing are eliminated (using this procedure), pigeons do not respond based on the local reinforcement history but instead develop a strong stimulus bias. Interestingly, the strategy of responding to the overall percentage correct for S1 or S2 was a slightly better strategy to maximize reinforcement in this experimental paradigm. The development of a win-stay/lose-shift response rule would have resulted in a maximum reinforcement of 80.6% whereas the average overall percent correct with this procedure was 80.17, which was a nonsignificant difference *t*(5) = .80, *p* = .46. Therefore, the preference to choose the S2 stimulus, which is arguably a less cognitively demanding task than the development of a win-stay/lose-shift rule, resulted in a comparable amount of overall reinforcement.

Section 5

Experiment 4

Equal probability of reversal or no reversal after Trial 3

In Experiment 3, the probability of a reversal occurring on a given trial within a sequence was equated, but with equal probability that a reversal could occur on any given trial, the total number of S2 correct trials was considerably greater than S1 correct trials. To reduce the bias to choose S2 and to provide a better comparison with the procedure used in the first 5-trial sequence experiment, Experiment 4 was designed such that a reversal occurred on Trial 1, Trial 4, or not at all; however, as in Experiment 3, the probability of a reversal or no reversal was equated at each point in the sequence at which a reversal could occur. Thus, in each block of 4 sequences there was one all S1 sequence, one sequence with a reversal at Trial 4, and 2 all-S2 sequences (see Table 4). The major difference between this procedure and the procedure used in Experiment 3 is that the overall probability that S2 was correct was reduced from 80.6% to approximately 60%. Therefore, it should have been less likely that subjects would develop a strong preference for the S2 stimulus rather than developing control by local reinforcement history. Because the ability to use time (or trial number) into the sequence was made unreliable as a cue, it was unlikely that the pigeons would use it as a basis of choice.

Additionally, with this particular procedure, if a reversal did not occur on Trial 1, it would not occur on Trials 2 or 3, and if it did not occur on Trial 4, it would not occur at all. Therefore, given that S1 was correct on Trial 1, subjects also should respond to S1 on Trials 2 and 3, and given that S1 was correct on Trial 4 they also should respond to S1 on Trial 5 as well. Additionally, if S2 were correct on Trial 1, it would be correct throughout the sequence. Therefore, had the pigeons used the cues provided by local feedback, regardless of which stimulus was chosen on Trial 1, subjects should have shifted

Table 4

Experiment 4: Probability of S1 Correct as a Function of Sequence Type and Trial Number

Sequence Type	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	S1 Corr. Per Sequence	Number of Sequences Per Block
1	S1	S1	S1	S1	S1	100%	1
2	S1	S1	S1	S2	S2	60%	1
3	S2	S2	S2	S2	S2	0%	2
S1 Corr. Per Trial Over Each Block	50%	50%	50%	25%	25%		4 Total

responses to S2 on Trials 2-5. This final task was included as a way to assess whether subjects would treat the sequences differently, depending on the location of the reversal or whether a reversal occurred or not.

Method

Subjects

Four White Carneaux pigeons (*Columbia Livia*) ranging in age from 2 to 12 yrs and two homing pigeons (*Columbia Livia*), which were approximately 1 yr old at the start of testing, served as subjects. All subjects had similar experience in previous experiments with discrimination learning but had not been exposed to a reversal-learning task. Subjects were housed and maintained in the same manner as in previous experiments.

Apparatus

The experiment was conducted using the same apparatus as in the previous studies.

Procedure

Subjects were exposed to the reversal procedure using the 5-trial paradigm in which a reversal occurred on Trial 4 of a sequence, or in which sequences were all S1+ or S2+. This manipulation eliminated the use of time as a reliable cue, as in Experiment 3; however, in Experiment 4, the only reversal that could be experienced during a sequence was in the middle of the sequence. Therefore, this procedure is a hybrid of the procedure used in the original experiment (Rayburn-Reeves, Molet, & Zentall, 2011; Experiment 1) in which a reversal occurred at a fixed location during the sequence and Experiment 3 in which a hazard function was used to equate for the probability of a reversal occurring on a given trial. In Experiment 4, subjects were exposed to blocks of 4 sequences in which two of the 4 sequences per block had a session in which only S2 was reinforced (reversal on Trial 1), one sequence in which the reversal occurred on Trial 4, and one sequence in which S1 was correct for the entire sequence. Each session consisted of 4 4-sequence blocks and there were for 60 sessions of training (240 blocks total).

Results

The results of Experiment 4 indicate that when pigeons are given a series of sequences in which a reversal occurs on Trial 1 on half of the reversals, and on Trial 4 or no reversal on one fourth of the trials each, thus making the overall likelihood of S2 correct approximately 60%, subjects show equal responding to S1 and S2 on Trial 1 and then show a slight bias to choose S2 on Trials 2-5 (see Figure 17). Furthermore, and consistent with the results of the previous three experiments, there was no difference in performance on sequences with reversals and no reversals. This finding is most surprising because only one of the four sequences involved a reversal. Therefore, if on Trial 1, S1 was correct, it would always be correct on Trials 2 and 3. If it continued to be correct on Trial 4, then it would always be correct on Trial 5 as well. As with Experiments 2 and 3, if S2 were correct on Trial 1, it would be correct for the remainder of the sequence. Therefore, the outcomes of early trials provided certainties about the consequences of future responses; however, there was no indication that subjects were using that information.

The data for each sequence type again was pooled over sequences to compare the overall probability of choice of S1 with the pigeon's performance (see Figure 18). A single sample t-test was conducted on the data for each trial relative to the overall probability that S1 was correct. The average choice of S1 (M, 50.74; SEM, 1.38) was not significantly different than the overall mean correct for Trial 1 (50%), *t*(5) = 0.53, *p* = .62; however, the average choice of S1 for Trial 2 (M, 41.42; SEM, 2.88) was significantly lower than the overall mean correct (50%), *t*(5) = -2.98, *p* = .03. On Trial 3,

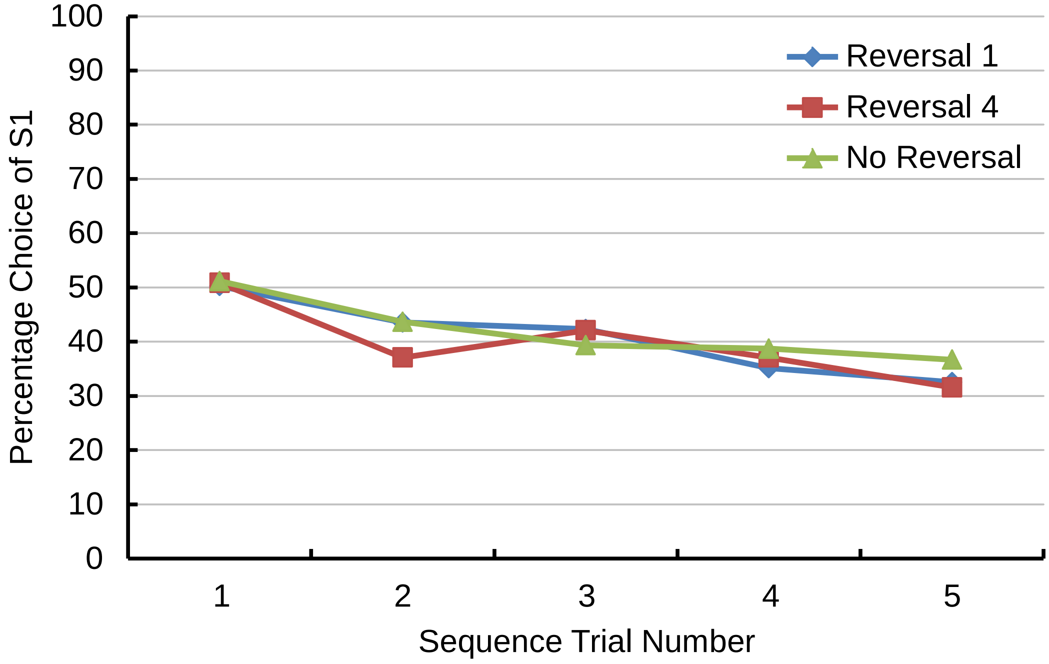

Figure 17. Experiment 4. Percentage choice of S1 as a function of sequence trial number averaged across subjects and across Sessions 41-60 for each sequence type.

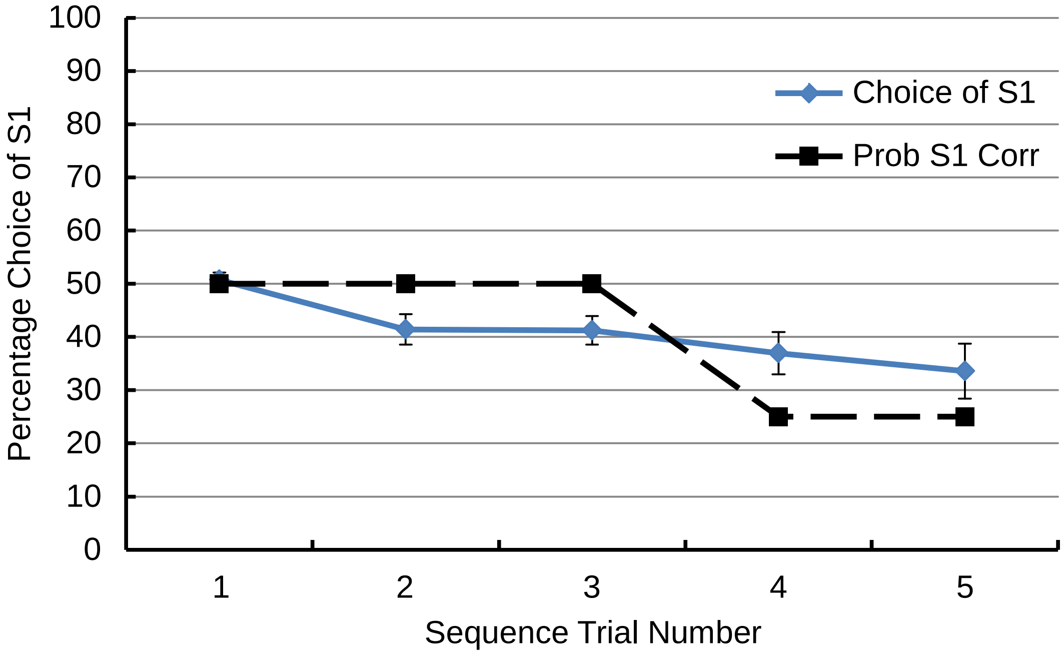

Figure 18. Experiment 4. Percentage choice of the first correct stimulus as a function of trial number collapsed across sequence types. The black dotted line indicates the overall probability of S1 correct as a function of trial number independent of reversal location.

the average choice of S1 (M, 41.23; SEM, 2.68) was again significantly lower than the overall mean (50%), *t*(5) = -3.26, *p* < .02; and on Trial 4, the average choice of S1 (M, 36.96; SEM, 3.96) was significantly higher than the overall mean (25%), *t*(5) = 3.02, *p* = .03. Finally, for Trial 5, the average choice of S1 (M, 33.58; SEM, 5.17) was significantly higher than the overall mean (25%), *t*(5) = 1.66, *p* = .10. The data from individual subjects averaged across Sessions 41-60 for the three reversal locations appears in Figure 19. As can be seen in the figure, there was some variability across subjects in their preference for S1 or S2 across the 5 trials; however, there was virtually no variability across reversal locations for any subject, a finding that is consistent with the findings from Experiments 1, 2, and 3.

Discussion

Equating for the probability of a reversal occurring on a given trial during the sequence did not reduce the likelihood that subjects anticipated the reversal. There was a 50 percent chance that S1 or S2 would be correct on the first trial of the sequence. Due to the saliency of the beginning of a given sequence, subjects showed equal responding to both S1 and S2 on Trial 1, most likely due to an increase in proactive interference as has been found in previous research (Gonzalez, Brehend, & Bitterman, 1967). However, Trials 2 and 3 showed more responding to S2 than the overall probability of S2 correct on those trials. Interestingly, subjects showed a significant bias to choose S1 on Trials 4 and 5 as compared with the overall likelihood of S1 correct. Again, subjects showed no sensitivity to the information afforded by the outcome of the preceding trials even though this information could have provided a greater amount of overall reinforcement than was obtained in the current study. Regardless of which stimulus was chosen on Trial 1, subjects should have shifted responses to S2 from Trials 2-5 had they used the cues

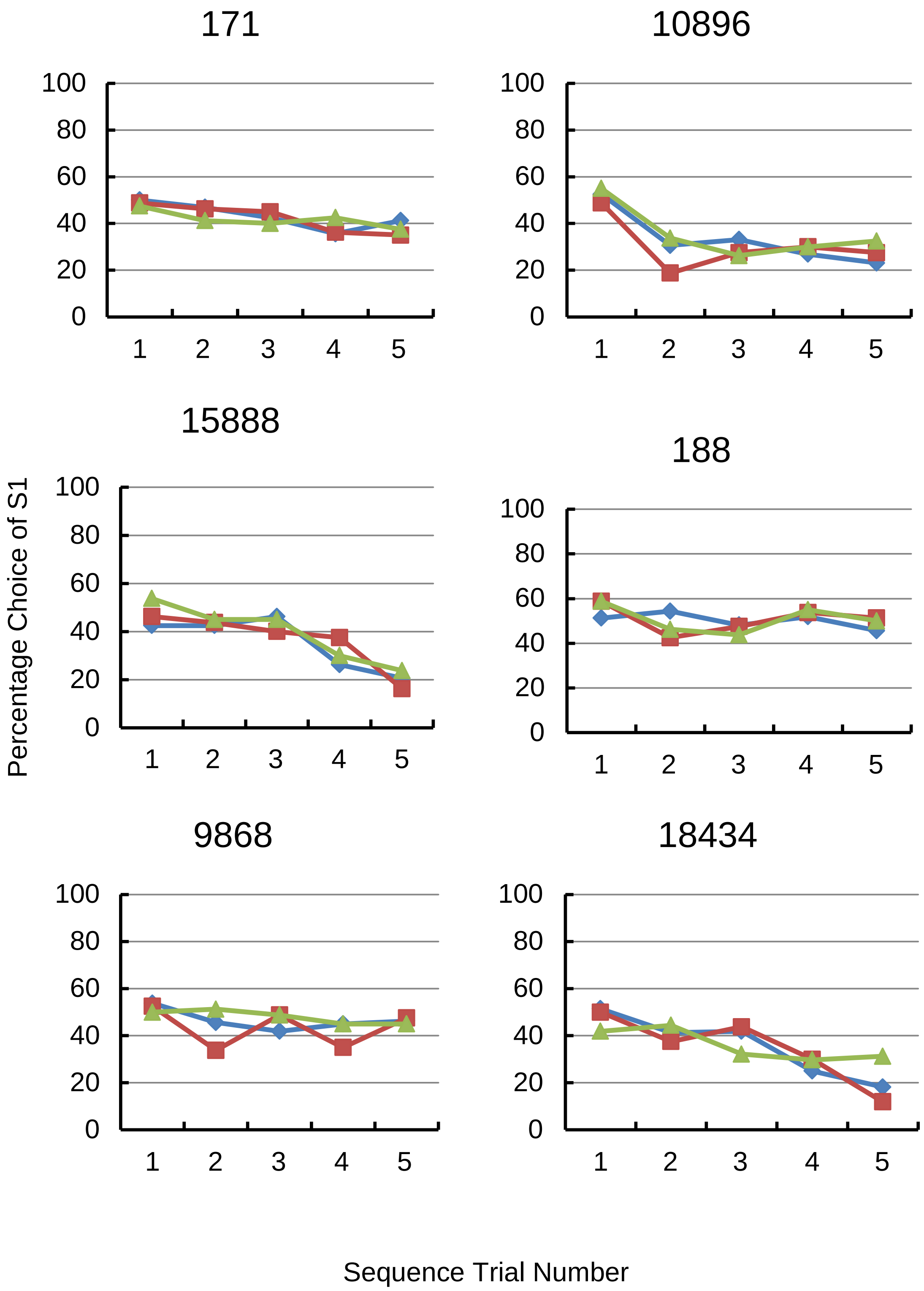

Figure 19. Experiment 4. Percentage choice of S1 as a function of sequence trial number for individual subjects averaged across Sessions 41-60 for each sequence type.

provided by local feedback. The development of a win-stay/lose-shift rule would have resulted in an overall percentage correct of 85; however, the average overall percentage correct across subjects was 53.18, significantly lower than the maximum amount possible, $t(5) = -31.69$, $p < .0001$. Given these constraints, it is interesting that pigeons did not show differing functions for the three sequence types. This particular procedure should have given pigeons the best opportunity to use the information afforded by the consequences of preceding trials as a basis for which stimulus would be correct; however, as with the previous experiments, pigeons did not show sensitivity to the reinforcement conditions as it pertained to immediate feedback.

It was also possible that, with the present procedure, the seldom occurrence of the reversal could have made the reversals difficult to discriminate. Because S2 was correct more often than S1 overall, it is possible that the subjects became sensitive to this difference and began to respond to S2 more often during early trials in the sequence; however, this does not explain the perseveration on later trials. Rather, it appears that subjects maintained responses to S1 and S2 equally on Trial 1 and then began responding to S2 somewhat more often as the trials progressed in a sequence.

Section 6

General Discussion

Taken together, the purpose of these four experiments was to explore procedures that might enhance pigeons' sensitivity to the consequences of prior choices. Specifically, the goal of these experiments was to create a procedure that increased the saliency of the response and outcome on each trial to determine their effect on reversal learning. Additionally, these experiments investigated whether a particular source of control, local reinforcement history, which would maximize overall reinforcement, would be used with 5-trial sequences instead of other sources of control, such as timing, which appeared to control choice in previous experiments with 80-trial sessions. In all four experiments, it was found that pigeons did not use the cues provided by the local history of reinforcement as evidenced by the fact that they responded in the same manner on all trials in each of the sequences, regardless of where (or whether) the reversal occurred. Instead, pigeons appeared to base their choices on the overall probability of reinforcement as a function of which trial they were on within the sequence. Experiment 1 showed this trend most clearly. In addition to probability matching, the pigeons also tended to show a bias to choose S2 more often than S1, a strategy not easily explained by probability matching alone. Experiment 3 was the only experiment in which pigeons obtained the maximum amount of reinforcement, and this was because subjects developed a preference for the S2 stimulus which, overall, yielded approximately 80% reinforcement.

It is not obvious why pigeons tended to use the overall probability of reinforcement for S1 or S2 across sequences as the basis of their choice when another cue, local reinforcement history, was available and would have produced a greater amount of reinforcement. What seems to be a consistent finding across all experiments conducted with pigeons on the within-session reversal task is that generally, pigeons are not using the optimal (local) available information and instead, appear to rely on other cues, such as timing or overall probability of reinforcement, which involve averaging over sessions.

In all experiments, the overall choice of S2 tended to increase as a function of trial number; however, the progressive choice of S2 across trials was most pronounced in Experiment 1, in which the overall probability of S2 increased from 0 to 100 across the five trials. It is possible that the within-session 5-trial sequence with which our pigeons were trained elicited a predisposed tendency to engage in foraging-like behavior. When foraging for food, where food is distributed in patches, the most appropriate behavior might be to remain at a particular patch for a particular time or based on some ratio between the amount of energy expended foraging and the amount of energy gained by the consumption of food (an optimal foraging account). These strategies may not be compatible with a procedure in which there is continuous reinforcement for the choice of one stimulus and then suddenly responding to a different stimulus is correct.

In all of our experiments, pigeons did not seem to base their responses on cues provided by the immediate feedback of reinforcement from the previous trial, even though the outcome could have served as a reliable conditional cue for which stimulus could be correct on the next trial. Research has shown that pigeons can learn conditional discriminations, such as matching-to-sample and oddity-from-sample tasks, to a high level of performance, where choice of a comparison stimulus is contingent upon the most recently presented sample stimulus. Pigeons can also learn to choose a comparison stimulus based on hedonic samples (food or no food) after being trained to associate one stimulus with the presentation of food and another with the absence of food (Zentall, Sherburne, & Steirn, 1992). With a conditional discrimination, an animal must be able to employ simple rules to solve the task (e.g., if food was just presented, choose red; if no food was presented, choose green). The ability for pigeons to learn to choose a comparison stimulus on the basis of the presence or absence of a food sample is especially interesting in light of the fact that in all of our experiments, the outcome from the previous trial, as well as the stimulus which was most recently chosen, which could have been used as a conditioned stimulus to indicate the next correct stimulus, was not used.

An even more complex form of conditional discrimination learning (called a biconditional discrimination) is one where a particular context cue, such as a house light, signals the conditional discrimination that is in effect on a given trial. For example, if the house light is on, then choice of a red comparison will be reinforced when red is the sample whereas if the house light is off and the sample is red, choice of the green comparison is reinforced (Edwards, Miller, & Zentall, 1985). In the limit, this procedure requires the animal to form essentially four independent, 3-chained rules to solve the task (i.e., if house light on, if red, choose red; if house light on, if green, choose green; if house light off, if red, choose green; if house light off, if green, choose red). In a sense, the biconditional discrimination task is comparable to the within-session reversal task used in my previous experiments. The house light cue, which served as the conditional cue to signal which contingency was in effect on a given trial in the biconditional task, is analogous to the outcome of the previous trial in the reversal task as it is the conditional cue to signal which contingency is in effect on the following trial. Similarly, in the biconditional task, the sample following the house light cue is a signal for which comparison will be reinforced, and is analogous to the previously pecked stimulus in the reversal task. Therefore, the same 3-chained rule could be used to solve the reversal task as with the biconditional task (i.e., if red, if food, choose red; if red, if no food, choose green; if green, if food, choose green; & if green, if no food, choose red). Therefore, although pigeons did not use these biconditional rules to solve the reversal task, there are a number of tasks that pigeons are able to perform that can be very complex and can require the use of rules to learn, which suggests that rule learning is not absent in the pigeon's cognitive repertoire.

One main difference between studies that have used the presence versus absence of food as sample stimuli in conditional discrimination tasks (where pigeons show rapid acquisition) and the results of our series of experiments with the reversal task is that, in our tasks, the outcome of the previous trial and the onset of the stimuli signaling the start of the next trial were separated by a 5-sec inter-trial interval. It may be that even the short (e.g., 5-sec) delay between the outcome of the previous trial and the onset of the stimuli which signal the following trial is sufficient to interfere with pigeons' ability to use the outcome of the previous trial as a conditional stimulus for choice of the correct comparison stimulus on the following trial. In light of the recent experiments with the within-session reversal task, it may be that pigeons do not readily develop rules based on local reinforcement history when the outcome of the preceding trial (and the stimulus associated with that outcome), which must be used as a basis for the next response, must be retained in short-term memory over a brief delay.

However, other procedures specifically designed to assess the ability for pigeons to use information from the previously reinforced response to maximize reinforcement have had some success. Williams (1972) used a procedure in which the overall probability of reinforcement associated with two stimuli was .50, but the local probability of reinforcement for repeating the same response was varied across trials, depending on the outcome of the previous trial. Specifically, the probability of reinforcement for repeating a response that was reinforced on the previous trial was .80, whereas switching to the alternative stimulus was reinforced with a probability of .20 (win-stay), whereas a non-reinforced response on the previous trial indicated that switching to the alternative stimulus resulted in a reinforcement with a probability of 1.0, while repeating the same response had a reinforcement probability of 0 (lose-shift). Results showed that, even though both components were learned, the lose-shift component was learned faster and better than the win-shift component; however, the probabilities associated with the lose-shift component were better differentiated (1.0 vs. 0) and the delay between trials in the lose-shift component was half as long as in the win-stay component (3 s vs. 6 s overall).

Shimp (1976), noting these differences, conducted a similar study in which the delay between trials was varied (2.5, 4, and 6 s) across trials for both components to assess the effects of delay between trials as a measure of the subject's ability to use the stimulus and outcome from the previous trial on the following trial. Additionally, he used a correction procedure in which incorrect responses resulted in a 5 s correction interval. That is, at the end of the interval, the trial was recycled until the subject made the correct response, thereby creating a situation where all trials ended in reinforcement. Results showed that subjects performed very well on both components, and the longer the delay between trials, the less accurately the subjects performed. Therefore, control by local reinforcement probability on choice of the following trial was evident and it was less effective as the delay between trials increased. Shimp (1976) interpreted this finding as the ability for pigeons to use the short-term memory for recent events to predict the likelihood of reinforcement for future behavior. These two studies indicate that pigeons are able to use the outcome of the previous trial as a basis for subsequent behavior and that memory for the stimulus and outcome is susceptible to very small changes in the delay between trials.

Further research has similarly suggested that improvement across reversals is greater with short (e.g., 6 s) as opposed to long (e.g., 60 s) inter-trial intervals (Ploog &

Williams, 2010; Randall & Zentall, 1997; Williams, 1971, 1976). Williams (1976) explained this finding as evidence that subjects can use the conditional cue of the previous trial’s outcome as a basis for response and that the cue is forgotten with longer intervals between trials. Williams further added that the ability to utilize previously presented outcomes as conditional stimuli may differ greatly across non-human animals and that this difference might, in part, contribute to the differences in improvement of reversal learning across species (p. 429). Support for this claim has come from studies showing significantly more rapid learning by corvids over problems in learning set tasks, as well as more rapid improvement over reversals in a serial reversal task by rooks, as compared with pigeons (Wilson, 1978). Similarly, it has been shown that jackdaws perform more accurately than pigeons over a series of delays on conditional discrimination tasks using food and no food samples (Wilson & Boakes, 1985).

The fact that pigeons did not seem very sensitive to the information afforded by local feedback in all of our experiments but seemed to rely on the overall probability of reinforcement across multiple sequences, suggests that the procedures under which we tested our pigeons did not evoke a rule-based strategy using cues from the local history of reinforcement. In the Williams (1972) and Shimp (1976) studies, however, the only information that could have been used to deviate from chance performance was the information afforded by the previous trial’s outcome. In our studies, other variables, such as timing and probability learning, could have also been used to facilitate learning about the changes in contingencies. In our original experiment, in which the reversal consistently occurred in the middle of the session, pigeons achieved above 90% accuracy overall using a time-based strategy. Even with the variable reversal procedures in

Experiments 1 and 2 with 5-trial sequences, the use of the overall probability of reinforcement on a given trial served to create above chance performance across sequences (70% overall reinforcement in Experiment 1, and 59.2% in Experiment 2), even though the maximum amounts of reinforcement (80, and 83.33%) were not achieved. Therefore, it is possible that alternative sources of control that increased the probability of overall reinforcement above 50% in the reversal procedures served to interfere with the use of local reinforcement cues. Additionally, it is possible that the delay between the outcome of the previous trial and the onset of the stimuli signaling the start of the next trial is sufficient enough to cause confusion about the use of information of a previous trial as the basis for the correct response on the following trial. That is, it may not be apparent that the trials separated by a dark delay are not independent of one another. The saliency of the dark delay between trials may serve as a cue indicating trial separation and therefore interfere with the use of the outcome of one trial as a conditional cue for the next correct response.

In the variable, within-session reversal procedure, it appears that pigeons were using an aggregate reinforcement history for S1 and S2, with the values of those aggregates changing as a function of time or trial number in the sequence. This type of behavior more closely resembles rules for abandoning a particular patch in lieu of another based on a fixed amount of time and energy consumption (Valone & Brown, 1989). Although one might think that keeping track of overall probability based on the time or trial number within a session or sequence would seem more difficult than employing the use of a win-stay/lose-shift rule, it may be that this ability for tracking changing probabilities as a function of time or events is a more natural ability for pigeons than one that requires the use of rules based on cues provided by the immediate feedback of the preceding trial's outcome.

Based on the series of experiments conducted using the within-session reversal learning task in pigeons, one might argue that the task may be too difficult for a non-human animal to solve using rules based on the immediacy of reinforcement; however, it is important to note that we have conducted a spatial midsession reversal experiment with rats under very similar procedures (with the exception that rats responded to levers instead of key lights) and found qualitatively different results (Rayburn-Reeves, Stagner, Kirk, & Zentall, in press; Experiment 2a). Specifically, rats showed no anticipation prior to the reversal and very rapid switching to S2 after the reversal (see Figure 20), suggesting that rats were using the immediate feedback afforded by the consequences of recent trials as a basis for responding to S1 and S2 and they were not using the time within the session as a cue. We also ran the variable within session reversal task with rats and found that, regardless of where the reversal occurred during the session, rats responded to S1 until the reversal trial, and then began responding to S2 almost immediately. Therefore, rats showed no evidence of using the time within the session as a cue and instead appeared to use the most appropriate cue to maximize reinforcement (Rayburn-Reeves, et al., in press; Experiment 2b).

Consistent with our findings that pigeons were not able to perform as accurately on the within-session reversal task as rats, other research has shown that rats also display a faster rate of reversal learning on serial reversal tasks (Bitterman, 1975; Mackintosh & Cauty, 1971) and often achieve a higher asymptote of performance (fewer errors to

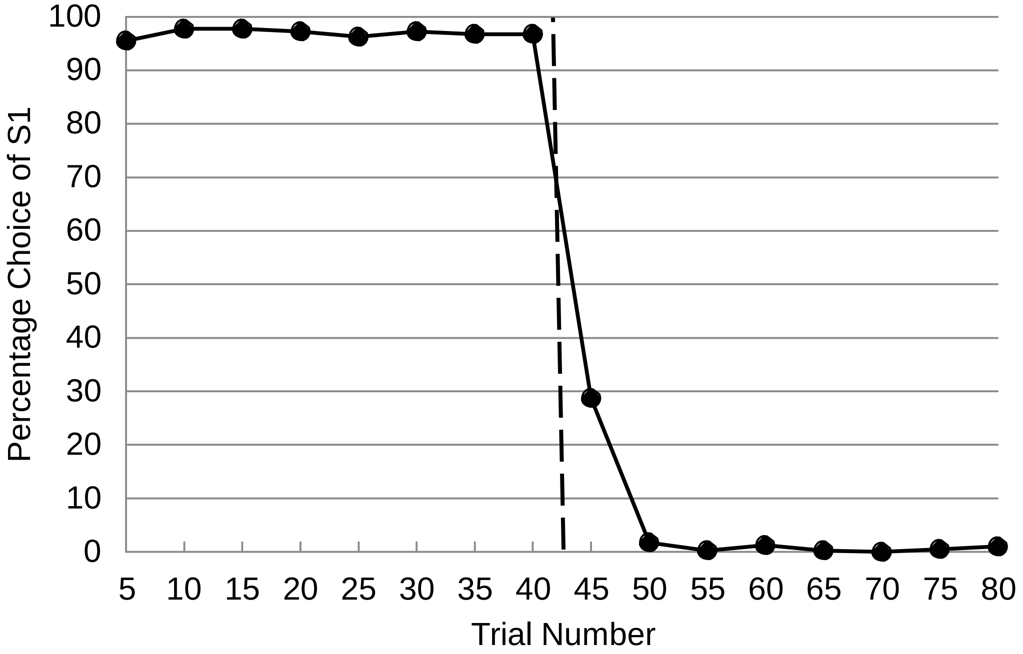

Figure 20. Midsession spatial reversal with rats. Percentage choice of S1 as a function of trial number averaged across subjects and Sessions 41-50. Data are plotted in blocks of 5 trials. The black dotted line indicates the reversal location.

criterion performance over reversals) than pigeons, especially when rats are trained using olfactory cues as opposed to visual or auditory cues (Nigrosh, Slotnick, & Nevin, 1975).

Consistent with the results of our research with rats, other research on serial reversal learning has found evidence that rats eventually learn to reverse responding in fewer than two trials (Dufort, Gutman & Kimble; 1954; Mackintosh, et al., 1968; Nigrosh, Slotnick, & Nevin, 1975). The benefit of the midsession reversal task, as opposed to the traditional serial reversal task that has been the most popular paradigm to study differences across species, is that in the serial reversal task, any differences found between species have been in the amount of improvement across reversals, which is an inherently quantitative measure. That is, if it is found that rats show greater improvement across reversals and eventually make fewer errors than pigeons, this difference does not say anything about the cognitive mechanisms behind the different performances. With the midsession reversal procedure, however, we found that the differences in performance between pigeons and rats were suggestive of a qualitative difference in the cognitive mechanism or information that was used to solve the task. Therefore, although not initially intended as such a procedure, the midsession reversal task might provide a more sensitive measure for the differences across species in their ability to maximize reinforcement, based on particular strategies.

One possibility for why rats might be more efficient at switching responses from one alternative to the other, based on limited experience with the reversed contingencies, may be due to the differences between pigeons and rats' foraging strategies. Rats are omnivores, which mean that the types of foods they can eat are extremely diverse. Additionally, the primary foods that they eat are often located in small quantities and in a variety of different and often irregular (unpredictable) locations in which they inhabit (Bond, Cook, & Lamb, 1981). Due to the diversity in location, quantity, and the nature of the food (plant or animal), rats therefore may more readily abandon locations or responses that previously provided reinforcement within a single or a few experiences with nonreinforcement. In contrast to rats, pigeons are granivores, which means that their food sources are not only more limited in kind, but also in location. Typically, pigeons will flock to certain locations in which food is available in abundance (e.g., open grasslands and agricultural areas) and in which a single visit does not deplete all of the food available in that location (Bond, et al., 1981). Additionally, pigeons, unlike rats, rely on the presence of other members of their species to signal the availability of foods and rarely forage to unknown places on their own. As Bond et al. (1981) state, "…individual flocks develop traditional feeding sights, areas that have proved in the past to provide abundant food and safety from predation" (p. 575). It is possible that the difference in the flexibility between the types of food eaten and the location of that food between rats and pigeons may contribute to their propensity to use particular strategies in tasks that require a very flexible behavioral strategy.

Other avian species that have also been shown to improve across serial reversals more rapidly and show greater improvement in learning set tasks than pigeons are certain species of corvid, such as rooks and crows (Wilson, 1978). This finding is particularly interesting because both of these corvid species, similar to rats, are omnivores. It may be that animals that have evolved to consume extremely diverse foods evolved to be able to more readily use flexible cognitive strategies, such as rule learning, with certain tasks that use food as reinforcement (Bond, Kamil, & Balda, 2007). It would be interesting know if other avian species whose food repertoires and foraging strategies are more diverse than pigeons would more readily adopt the appropriate strategies on the within-session reversal task, or whether other available cues, such as timing or probability matching, would gain control of behavior. In the limit, it appears that the design of our tasks, which require the pigeon to use an outcome from a previous trial to solve the next, does not appear to allow pigeons to readily adopt that cue in lieu of other cues that may provide information about patterns of reinforcement.

References

Benowitz, L., and Teng, E. L., (1973). Contrasting effects of three forebrain ablations on discrimination learning and reversal in chicks. *Journal of Comparative and Physiological Psychology*, *84*, 391-397.

Beran, M. J., Klein, E. D., Evans, T. A., Chan, B., Flemming, T. M., Harris, E. H., Washburn, D. A., & Rumbaugh, D. M. (2008). Discrimination reversal learning in capuchin monkeys (*Cebus apella*). *The Psychological Record*, *58,* 3-14.

Bitterman, M. E. (1965). Phyletic differences in learning. *American Psychologist*, *20,* 396-410.

Bitterman, M. E. (1969). Habit-reversal and probability learning: rats, birds, and fish. In R. M. Gilbert & N. S. Sutherland (Eds.), *Animal discrimination learning.* New York: Academic Press.

Bitterman, M. E. (1975). The comparative analysis of learning. *Science*, *188*, 699-709.

Bitterman, M. E., Wodinsky J., & Candland, D. K. (1958). Some comparative psychology. *American Journal of Psychology*, *71*, 94–110.

Bond, A. B., Cook, R. G., & Lamb, M. R. (1981). Spatial memory and the performance of rats in the radial-arm maze. *Animal Learning & Behavior*, *9* (4), 575-580.

Bond, A. B., Kamil, A., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of north American corvids (*Gymnorhinus cyanocephalus, Nucifraga Columbiana, Aphelocoma californica*). *Journal of Comparative Psychology*, *121* (4), 372-379.

Bullock, D. H., & Bitterman, M. E. (1962). Habit reversal in the pigeon. *Journal of Comparative and Physiological Psychology*, *55*, 958-962.

Bushnell, P. J., & Stanton, M. E. (1991). Serial spatial reversal learning in rats: Comparison of instrumental and automaintenance procedures. *Physiology & Behavior, 50* (6), 1145-1151.

Cronholm, J. N., Warren J. M., & Hara, K. (1960). Distribution of training and reversal learning by cats. *Journal of Genetics and Psychology*, *96*, 105–113.

Datta, L. G., Milstein, S., & Bitterman, M. E. (1960). Habit reversal in the crab. *Journal of Comparative and Physiological Psychology*, *53*, 275–278.

Deterline, W. A. (1957). Operant discrimination reversals: Comparative data. *Journal of the Experimental Analysis of Behavior*, *3* (3), 247-253.

Dews, P. B. (1957). Studies on behavior. III. Effects of scopolamine on reversal of a discriminatory performance in pigeons. *Journal of Pharmacology and Experimental Therapeutics*, *119***,** 343–353.

Doty, B. A., & Combs, W. C. (1969). Reversal learning of object and positional discriminations by mink, ferrets and skunks. *Quarterly Journal of Experimental Psychology*, *21*, 58–62.

Dufort, R., Guttman, N., & Kimble, G. (1954). One-trial discrimination reversal in the white rat. *Journal of Comparative and Physiological Psychology*, *7*, 248-249.

Duncan, H., & Slotnick, B. M. (1990). Olfactory and visual reversal learning in the pigeon. *Chemical Senses*, *15*, 59-73.

Durlach, P. J., & Mackintosh, N. J. (1986). Transfer of serial reversal learning in the pigeon. *Quarterly Journal of Experimental Psychology, 36B,* 81-95.

Edwards, C. A., Miller, J. S., & Zentall, T. R. (1985). Control of pigeons' matching and mismatching performance by instructional cues. *Animal Learning & Behavior*, *13*, 383-391.

Gonzalez, R., Brehend, E., & Bitterman, M. (1967). Reversal learning and forgetting in bird and fish. *Science*, *158*, 519-521.

Gossette, R. L., Gossette, M. F., & Riddell, W. (1966). Comparisons of successive discrimination reversal performances among closely and remotely related avian species. *Animal Behaviour, 14* (4), 560-564.

Harlow, H. F. (1949). The formation of learning sets. *Psychological Review*, *56* (1), 51-65.

Holmes, P. A., & Bitterman, M. E. (1966). Spatial and visual habit reversal in the turtle. *Journal of Comparative and Physiological Psychology*, *62* (2), 328-331.

Hulse, S. H., Egeth, H., & Deese, J. (1980). *The Psychology of Learning*. McGraw-Hill, New York.

Kay H., & Sime, M. E. (1962). Discrimination learning with old and young rats. *Journal of Gerontology*, *17*, 75–80.

Kirk, K. L., & Bitterman, M. E. (1963). Habit reversal in the turtle. *Quarterly Journal of Experimental Psychology*, *15*, 52–57.

Levine, M. (1965). Hypothesis behavior. In A. M. Schrier, H. F. Harlow, & F. Stollnitz (Eds.), *Behavior of nonhuman primates* (Vol. 1, pp. 97-127). New York: Academic Press.

Mackintosh, N. J. (1988). Approaches to the study of animal intelligence. *British Journal of Psychology*, *79* (4), 509-526.

Mackintosh, N. J., & Cauty, A. (1971). Spatial reversal learning in rats, pigeons and goldfish. *Psychonomic Science, 22*, 281-282.

Mackintosh, N. J., & Holgate, V. (1969). Serial reversal training and nonreversal shift learning. *Journal of Comparative and Physiological Psychology*, *67,* 89-93.

Mackintosh, N. J., & Little, L. (1969). Selective attention and response strategies as factors in serial reversal learning. *Canadian Journal of Psychology*, *23*, 335-345.

Mackintosh, N. J., & Mackintosh, J. (1964). Performance of Octopus over a series of reversals of simultaneous discrimination. *Animal Behaviour*, *12*, 321-324.

Mackintosh, N. J., McGonigle, B., Holgate, V., & Vanderver, V. (1968). Factors underlying improvement in serial reversal learning. *Canadian Journal of Psychology, 22*, 85-95.

Mackintosh, N. J., Wilson, B., & Boakes, R. A. (1985). Differences in mechanisms of intelligence among vertebrates. *Philosophical Transactions of the Royal Society, London*, *308B*, 53-66.

Macphail, E. M. (1972). Within-day serial reversal of a position discrimination by pigeons. *Quarterly Journal of Experimental Psychology*, *24*, 200-206.

Martin, T. I., Zentall, T. R., & Lawrence, L. (2006). Simple discrimination reversals in the domestic horse: Effect of discriminative stimulus modality on learning to learn. *Applied Animal Behaviour Science, 101*, 328-338.

McDowell, A. A., Brown W. L., & White, H. F. (1961). Oddity reversal and delayed response performance of monkeys previously exposed to focal head irradiation. *Journal of Genetic Psychology*, *99*, 75–81.

Nigrosh, B. J., Slotnick, B. M., & Nevin, J. A. (1975). Olfactory discrimination, reversal learning, and stimulus control in rats. *Journal of Comparative and Physiological Psychology, 89* (4), 285-294.

North, A. J. (1950). Improvement in successive discrimination reversals. *Journal of Comparative and Physiological Psychology, 43*, 442–460.

Papini, M. R., & Ishida, M. (1998). Comparative psychology of learning: Recent issues and problems. *Memoirs of Osaka University, 47* (1), 1-9.

Peters, E. H. (1981). Differentiation and syntax in the evolution of behavioral flexibility. *Current Anthropology, 22* (6), 683-686.

Ploog, B. O., & Williams, B. A. (2010). Serial Discrimination Learning in pigeons as a function of inter-trial interval and delay of reinforcement. *Learning & Behavior, 38* (1), 96-102.

Pubols, B. H. (1956). The facilitation of visual and spatial discrimination reversal by overlearning. *Journal of Comparative and Physiological Psychology, 49*, 243-248.

Rajalakshmi, R., & Jeeves, M. A. (1965). The relative difficulty of reversal learning (reversal index) as a basis of behavioural comparisons. *Animal Behaviour, 13* (2-3), 203-211.

Randall, C. K., & Zentall, T. R. (1997). Win-stay/lose-shift and win-shift/lose-stay learning by pigeons in the absence of overt response mediation. *Behavioral Processes, 41*, 227-236.

Rayburn-Reeves, R. M., Stagner, J. P., Kirk, C. R. & Zentall, T. R. (in press). Reversal learning in rats (*Rattus norvegicus*) and pigeons (*Columba livia*): Qualitative differences in behavioral flexibility. *Journal of Comparative Psychology*.

Rayburn-Reeves, R. M., Molet, M., & Zentall, T. R. (2011). Simultaneous Discrimination Reversal Learning in Pigeons and Humans: Anticipatory and Perseverative Errors. *Learning & Behavior, 39* (2), 125-137.

Rayburn-Reeves, R. M., Miller, H. C., & Zentall, T. R. (2010) "Counting" by Pigeons: Discrimination of the number of biologically relevant sequential events. *Learning & Behavior*, *38*, 169-176.

Reid, R. L. (1958). Visual discrimination in pigeons. *Journal of Comparative and Physiological Psychology*, *51*, 716-720.

Reid, I. C., & Morris, R. G. M. (1992). Smells are no surer: Rapid improvement in olfactory discrimination is not due to the acquisition of a learning set. *Biological Sciences*, *247*, 137-143.

Saunders, J. C., Chen, C., & Pridmore, P. A. (1971). Successive habit-reversal in momotreme *Tachyglossus Aculeatus* (echidna). *Animal Behavior*, *19*, 552-555.

Schrier, A. M., & Thompson, C. R. (1984). Are learning sets learned? *Animal Learning & Behavior*, *12*, 109–112.

Schusterman, R. J. (1966). Serial discrimination-reversal learning with and without errors by the California sea lion. *Journal of the Experimental Analysis of Behavior, 9* (5), 593-600.

Shimp C. P. (1976). Short-term memory in the pigeon: The previously reinforced response. *Journal of the Experimental Analysis of Behavior, 26*, 487-493.

Seidman, E. (1949). Relative ability of newt and terrapin to reverse a direction habit. *Journal of Comparative and Physiological Psychology*, *42*, 320–327.

Slotnick, B. M., & Katz, H. (1974). Olfactory learning-set formation in rats. *Science*, *185*, 796–798.

Slotnick, B. M., Kufera, A., & Silberberg, A. M. (1991). Olfactory learning and odor memory in the rat. *Physiology & Behavior*, *50*(3), 555-561.

Staddon, J. E. R., & Frank, J. (1974). Mechanisms of discrimination reversal in pigeons. *Animal Behavior*, *22* (4), 820-828.

Stenhouse, D. (1974). The evolution of intelligence: A general theory and some of its implications. Barnes & Noble Books, New York.

Thomas, R. K. (2006). An Examination of Fundamental Differences Between Conceptualization and Learning Set Formation. Found online at http://rkthomas.myweb.uga.edu/ConceptVersusLS.htm 1/11/2010

Valone T.J., & Brown J.S. (1989). Measuring patch assessment abilities of desert granivores. *Ecology*, *70*, 1800-1810.

Warren, J. M. (1965). The Comparative Psychology of Learning. *Annual Review of Psychology*, *16*, 95-118.

Warren, J. M. (1966). Reversal learning and the formation of learning sets by cats and rhesus monkeys. Journal of Comparative and Physiological Psychology, 61 (3), 421-428.

Watson, D. J., Sullivan, J. R., Frank, J. G., & Stanton, M. E. (2005). Serial reversal learning of position discrimination in developing rats. Wiley Periodicals Inc. (Article published online) www.interscience.wiley.com

Williams, J. T. (1967). Efficient motivation for studying crocodilian learning. *Psychonomic. Science*, *8*, 279.

Williams, B. A. (1971). The effects of inter-trial interval on discrimination reversal learning in the pigeon. *Psychonomic Science, 23,* 241-243.

Williams, B. A. (1972). Probability learning as a function of momentary reinforcement probability. *Journal of the Experimental Analysis of Behavior, 17* (3), 363-368.

Williams, B. A. (1976). Short-term retention of response outcome as a determinant of serial reversal learning. *Learning and Motivation*, *7,* 418-430.

Wilson, B. J. (1978). *Complex learning in birds*. Unpublished doctoral dissertation, University of Sussex, Brighton, England.

Wilson, B., & Boakes, R. A. (1985). A comparison of the short-term memory performances of pigeons and jackdaws. *Learning & Behavior, 13* (3), 285-290.

Wodinsky, J. & Bitterman, M. E. (1957). Discrimination reversal in the fish. *American Journal of Psychology, 70*, 569–576.

Woodard, W., Schoel, W., & Bitterman, M. (1971). Reversal Learning with singly-presented stimuli in pigeons and goldfish. *Journal of Comparative and Physiological Psychology*, *76*, 460-467.

Zentall, T. R., Sherburne, L. M., & Steirn, J. N. (1992). Development of excitatory backward associations during the establishment of forward associations in a delayed conditional discrimination by pigeons. *Animal Learning & Behavior, 20*, 199-206.

Vita

Rebecca Marie Rayburn-Reeves

Date and Place of Birth:
July 24th, 1982, in Hamilton, Ontario

Education

- Appalachian State University, Bachelor of Science in Psychology, Minor in Philosophy & Religion, May 2004

- University of North Carolina Wilmington, Master of Arts, Psychology, July 2007, Supervisor: Dr. Mark Galizio, August 2005-July 2007

Teaching and Research Experience

- Research Assistant to Dr. Philipp Kraemer, January 2011-December 2011

- Teaching Assistant, to Dr. Jonathon Golding, Introduction to Psychology Laboratory, August 2010-December 2010

- Laboratory Research Supervisor for Dr. Thomas R. Zentall, January 2009-June 2009

- Laboratory Research Supervisor for Dr. Thomas R. Zentall, August 2009-December 2009

- Teaching Assistant to Dr. Thomas Zentall, Animal Behavior Laboratory, January 2009-May 2009

- Teaching Assistant to Dr. Ron Taylor, Learning and Behavior Laboratory, August 2008-December 2008

- Laboratory Research Supervisor for Dr. Thomas R. Zentall, January 2008-August 2008

- Teaching Assistant to Dr. Larry Gottlob, Cognitive Psychology Laboratory, August 2007-December 2007

- Laboratory Research Assistant for Dr. Mark Galizio, January 2007-May 2007

- Teaching Assistant to Dr. Julian Keith, History of Psychology, August 2006-December 2006

- Teaching Assistant, Social Psychology, January 2006-May 2006
- Teaching Assistant to Dr. Mark Galizio, Drugs and Behavior, August 2005-December 2005

Professional Affiliations:

2005-2007	Southeastern Association for Behavior Analysis
2005-2011	Comparative Cognition Society
2009-2011	American Psychological Association

Awards

2008	Graduate Teaching Assistant of the Year, University of Kentucky
2006	Travel Grant, University of North Carolina, $400
2007-2011	Travel Grants, University of Kentucky, $400 per year
2009	Research Grant provided by University of Kentucky, $750
2003	2,000 Scholarship for academic excellence, Hound Ears Club

Selected Presentations

Rayburn-Reeves, R.M., Miller, H.C., Pattison, K.F., Stagner, J.P., & Zentall, T.R. (2009, November). My Dog is as Smart as Your Baby and Other Lessons from Comparative Cognition Research. Guest speaking presentation at the Kentucky Psychological Association, Fall 2009

Rayburn-Reeves, R.M., Bullard, L. A., Poerstal, L.B., Bruce, K.E., & Galizio, M. (2006, October). Evaluating Functional Classes in the Rat using Olfactory Stimuli and Class-Specific Reinforcers. Poster presented at the meeting of the South Eastern Association for Behavior Analysis, Greenville, SC.

Rayburn-Reeves, R.M., Thomas, R., Miller, L.L., & Galizio, M. (2007, March). Matching and non-matching to sample in rats with olfactory stimuli. Poster presented at the International Conference of Comparative Cognition, Melbourne, FL.

Rayburn-Reeves, R. M. & Zentall, T. R. (2008, April) Animal Memory: The Contribution of Generalization Decrement. Paper presented at the 22nd Annual Tri-State Convention, Albion, MI.

Rayburn-Reeves, R. M., Miller, H. C., & Zentall, T. R. (2008, November). Numerical Competence by Pigeons. Paper presented at the Comparative Cognition and Learning fall conference, Chicago, IL.

Rayburn-Reeves, R.M., Miller, H.C., & Zentall, T.R. (2010, March). Pigeons' Acquisition of a simultaneous-discrimination midsession reversal. Paper presented at the International Conference of Comparative Cognition, Melbourne, FL.

Rayburn-Reeves, R.M., Stagner, J.P., Kirk, C.R., & Zentall, T.R. (Spring 2011). Qualitative differences in Behavioral Flexibility between rats and pigeons. Paper presented at the International Conference of Comparative Cognition, Melbourne, FL.

Rayburn-Reeves, R. M., Stagner, J. P., & Zentall, T. R. (Spring 2011). The Monty Hall Dilemma: What birds can teach us about probability learning. Paper presented at the 24th Annual Tri-State Convention, Purdue, IN.

PUBLICATIONS

Miller, H.C., Gipson, C. G., Vaughan, A., **Rayburn-Reeves, R.,** & Zentall T. R. (2009). Object Permanence in Dogs: Invisible Displacement in a Rotation Task. *Psychological Bulletin and Review, 16(1),* 150-155.

Miller, H. C., **Rayburn-Reeves, R.**, & Zentall, T. R. (2009). Imitation and emulation by dogs using a bidirectional control procedure. *Behavioural Processes, 80(2),* 109-114.

Miller, H. C., **Rayburn-Reeves, R.**, & Zentall, T. R. (2009). What do dogs know about hidden objects? *Behavioural Processes*, 81(3), 439-446.

Rayburn-Reeves, R., & Zentall, T.R. (2009). Animal memory: The contribution of generalization decrement to delayed conditional discrimination retention functions. *Learning & Behavior, 37*, 299-304.

Rayburn-Reeves, R. M., Miller, H. C., & Zentall, T. R. (2010). "Counting" by Pigeons: Discrimination of the Number of Biologically Relevant Sequential Events. *Learning & Behavior, 38*(2), 169-176.

Miller, H. C., Pattison, K. F., DeWall, N. C., **Rayburn-Reeves, R.**, & Zentall, T. R. (2010). Self-Control without a "Self"?: Common Self-Control Processes in Humans and Dogs. *Psychological Science, 21*(4), 534-538.

Pattison, K. F., Miller, H.C., **Rayburn-Reeves, R.M.**, & Zentall, T. (2010). The case of the Disappearing Bone: Dogs' Understanding of the Physical Properties of Objects. *Behavioral Processes, 85*(3), 278-282.

Rayburn-Reeves, R.M., Molet, M., & Zentall, T.R. (2010). Simultaneous discrimination reversal learning in pigeons and humans: Anticipatory and Perseverative Errors. *Learning & Behavior, 39*(2), 125-137.

Rayburn-Reeves, R.M., Stagner, J.P., Kirk, C.R., Zentall, T.R. Reversal Learning in Rats and Pigeons: Qualitative differences in Behavioral Flexibility. *Journal of Comparative Psychology* (in press).